

JAN 5 - 1935

# ECOLOGICAL MONOGRAPHS

VOL. 5

JANUARY, 1935

NO. 1

OFFICIAL PUBLICATION OF THE  
ECOLOGICAL SOCIETY OF AMERICA

---

## CONTENTS

CHANGES IN THE OSMOTIC VALUE OF THE EXPRESSED  
SAP OF LEAVES AND SMALL TWIGS OF *LARREA*  
*TRIDENTATA* AS INFLUENCED BY  
ENVIRONMENTAL CONDITIONS

T. D. MALLERY

THE EFFECTS OF BLACK LOCUST ON ASSOCIATED  
SPECIES WITH SPECIAL REFERENCE  
TO FOREST TREES

A. G. CHAPMAN

THE ORIGINAL FOREST TYPES OF SOUTHERN  
NEW ENGLAND

STANLEY W. BROMLEY

---

PUBLISHED QUARTERLY BY  
THE DUKE UNIVERSITY PRESS  
DURHAM, N. C., U.S.A.

# ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL  
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

## EDITORIAL BOARD

R. E. COKER  
University of North Carolina  
Chapel Hill, N. C.

W. S. COOPER  
University of Minnesota  
Minneapolis, Minn.

A. E. EMERSON  
University of Chicago  
Chicago, Ill.

G. D. FULLER  
University of Chicago  
Chicago, Ill.

H. A. GLEASON  
New York Botanic Garden  
Bronx Park, New York, N. Y.

C. H. KENNEDY  
Ohio State University  
Columbus, Ohio

PAUL B. SEARS  
University of Oklahoma  
Norman, Oklahoma

A. H. WRIGHT  
Cornell University  
Ithaca, New York

## *Managing Editors*

*Botany*  
C. F. KORSTIAN  
Duke University  
Durham, N. C.

*Zoology*  
A. S. PEARSE  
Duke University  
Durham, N. C.

*Business Manager*  
Duke University Press  
Durham, N. C.

The editorial board of this journal will consider ecological papers which are long enough to make twenty-five printed pages or more. Shorter ecological papers should be submitted to the editor of *Ecology*, which is also published by the Ecological Society of America. Both journals are open to ecological papers from all fields of biological science.

Manuscripts should be typewritten and may be sent to any member of the Editorial Board. Proof should be corrected immediately and returned to the Managing Editor at the address given above. Reprints should be ordered when proof is returned. Fifty copies, without covers, are supplied to authors free; covers and additional copies at cost. Correspondence concerning editorial matters should be sent to the Managing Editor; that concerning subscriptions, change of address, and back numbers to the Business Manager.

Subscription price, \$6.00 per year. Parts of volumes can be supplied at the rates for single numbers, \$1.50 each. Missing numbers will be supplied free when lost in the mails if written notice is received by the Business Manager within one month of date of issue. All remittances should be made payable to the Duke University Press.

Agents in Great Britain: The Cambridge University Press, Fetter Lane, London, E. C. 4. Prices can be had on application.

Entered as Second-class Matter at the Postoffice at Durham, North Carolina.

COPYRIGHT, 1935, BY DUKE UNIVERSITY PRESS

# ECOLOGICAL MONOGRAPHS

VOL. 5

JANUARY, 1935

No. 1

## CHANGES IN THE OSMOTIC VALUE OF THE EXPRESSED SAP OF LEAVES AND SMALL TWIGGS OF *LARREA TRIDENTATA*<sup>1</sup> AS INFLUENCED BY ENVIRON- MENTAL CONDITIONS

By T. D. MALLERY<sup>2</sup>

*Desert Laboratory  
Carnegie Institution of Washington  
Tucson, Arizona*

<sup>1</sup> *Larrea tridentata* Cav. = *Covillea tridentata* (DC.) Vail.

<sup>2</sup> The writer gratefully acknowledges the helpful suggestions, kindly criticisms and other aid given him during the course of this investigation by Dr. Forrest Shreve, in charge of the Desert Laboratory; Dr. B. M. Duggar, University of Wisconsin; Dr. Heinrich Walter, University of Heidelberg; and Mr. R. A. Greene and Mr. H. V. Smith, University of Arizona.

## CONTENTS

	PAGE
INTRODUCTION .....	3
MATERIALS AND METHODS .....	5
Method of Collecting and Killing Leaf and Twig Samples .....	7
Method of Extracting the Sap .....	8
Determination of the Freezing Point .....	9
Calculation of the Osmotic Value .....	11
Soil Moisture Determinations and Rainfall Records .....	11
Soluble Salt Determinations .....	12
Mechanical Analysis of Soils .....	12
Chemical Analysis of Soils .....	12
Ash Analysis of Plants .....	13
Diurnal Variations in Osmotic Value .....	13
PRESENTATION AND DISCUSSION OF DATA .....	14
Reliability of the Method of Sampling .....	14
Seasonal Variations in Osmotic Values .....	15
Osmotic Values of <i>Larrea</i> as Influenced by Soil Moisture and Rainfall .....	18
Osmotic Values of <i>Larrea</i> in Relation to the Total Soluble Salt Content of the Soil .....	23
SUMMARY OF SEASONAL VALUES .....	24
Mechanical Analysis of Soils .....	25
Chemical Analysis of Soils for Alkali Salt Content .....	25
Ash Analysis of <i>Larrea tridentata</i> .....	25
Diurnal Changes in the Osmotic Value and Moisture Content of the Leaves and Small Twigs .....	26
Individual Differences in Osmotic Value Between <i>Larrea</i> Bushes in the Same Habitat .....	28
GENERAL DISCUSSION .....	28
SUMMARY AND CONCLUSIONS .....	32
LITERATURE CITED .....	33



# CHANGES IN THE OSMOTIC VALUE OF THE EXPRESSED SAP OF LEAVES AND SMALL TWIGS OF *LARREA TRIDENTATA* AS INFLUENCED BY ENVIRONMENTAL CONDITIONS

## INTRODUCTION

A great amount of experimental research has been done on the effect of environment upon the concentration of the cell sap of plants. The most noteworthy and extensive contributions to this phase of botanical research are those of the late J. Arthur Harris and his colleagues (1915-1921) who have emphasized the value of such work in ecological and phytogeographical studies.

One of the chief influences of the environment upon the cellular activity of a plant is manifested in changes in the moisture content of the plant tissues and many determinations of the moisture content of plants and of plant parts have been made for the purpose of obtaining a measure of this influence. However, such measurements indicate only the total moisture content of the tissues and do not give the distribution of that moisture. Measurements of the osmotic pressure of the cell sap, on the other hand, while they do not show the amount of water present, indicate the condition of the water, which is of far greater significance for the plant and much more indicative of the plant's welfare. All metabolic activities of a plant take place in solution and their rate is largely determined by the degree of saturation of the plant tissues. Determinations of the changes which occur in the concentration of the cell sap of a plant from time to time therefore furnish a very good indication of the influences of the environmental conditions upon the plant.

The term "osmotic value" is a better one to use when referring to the concentration of the cell sap, since the osmotic pressures obtained for plant tissues are always subject to the accuracy of the method used in determining them. Ursprung and Blum (1916) are credited with having originated the symbol "Ov" to designate this value.

Numerous investigations dealing with winter hardiness and with drought resistance have shown that each species of plant is limited in its response to environmental conditions by a definite range of osmotic values for its cell sap, and this range is specific for a given species. Recently, Walter (1929) has emphasized the fact that not only may each species of plant experience a range in osmotic values throughout which it can survive successfully, but that each species is characterized by a somewhat definite rate of change in the osmotic value of its sap as conditions for development become more favorable or less favorable to the individual plants. During the severe cold period which occurred from January to March 1929 in Europe, *Hedera helix*, with a range of osmotic values from 14 to 24 atmospheres, was killed while *Pinus silvestris*, which has the same osmotic inertia, was not killed. The latter

possesses a higher maximum value and the cold period broke before that maximum was reached. *Buxus sempervirens*, on the other hand, with a range of osmotic value from 33 to 72 atmospheres has less osmotic inertia than the other two species and the maximum osmotic value was just reached at the end of the period of extremely low temperatures and therefore only a small amount of killing of this plant occurred.

The purpose of the work herein reported is to determine the range and differences in the rate of change of osmotic values prevailing in *Larrea tridentata* under natural conditions of growth over a considerable period of time and to attempt to correlate these variations in range and rate of change with factors of the environment.

*Larrea tridentata* is commonly called "creosote bush" because of the creosote-like odor which is produced when the plants become wet. Erroneously the creosote bush is sometimes called greasewood.

Under usual conditions *Larrea tridentata*, which is placed in the Zygophyllaceae, appears as a dark brownish green shrub from 4 to 6 feet high. It is an open type of bush; the main branching occurs in the crown at the surface of the ground. The dark brownish green color is due partly to the thick resin-covered leaves and partly to the fact that during a greater part of the year a certain quantity of dead leaves are present on the bushes. The leaves are quite small and are most abundant on the young twigs.

Several reasons might be advanced for selecting *Larrea* for this investigation. One is its wide distribution in the southwest. Shantz and Piemeisel (1924) state that in the southwestern desert region the creosote bush association is the most important type of vegetation. Its range of distribution extends from the Mohave desert nearly to central Texas and in southwestern United States and northwestern Mexico. *Larrea* is found at all elevations from sea level to 4,000 feet.

The creosote bush, which is a non-succulent, slow growing, shrubby perennial, is very drought resistant, as might well be expected of a plant with such a distribution range. Harris and Lawrence (1916) made the observation that the occurrence of *Larrea* as the dominant plant over thousands of square miles of territory in the arid southwest is proof that it is one of the most successful of the desert perennials. The drought resistant qualities of this plant arouse even more profound respect when we realize that it inhabits the most xeric areas, excepting the salt spots, which the southwestern desert embraces; namely, the bajadas or outwash slopes.

Livingston, in the publication of Spalding (1909), while writing on the dryness of the bajadas, observes that this condition probably accounts for the absence here of almost all vegetation excepting the characteristic *Larrea* and a number of forms which are active only during the rainy seasons. In connection with his work on the root habits of desert plants, Cannon (1911) found that for the period of his studies the soil of the bajada did not contain

sufficient water for shallow-rooted plants for more than three weeks of the year. It appears therefore that the bajadas are very xeric habitats and that the creosote bush is the chief plant inhabitant of these areas.

Another reason for the selection of *Larrea tridentata* for these studies is the fact that it makes successful and persistent growth in relatively thin bodies of soil over layers of hardpan. In Arizona the hardpan, or caliche, as it has been called since the days of the early Spanish settlers, is always calcareous in nature and, as pointed out by Breazeale and Smith (1930) is formed by the solution, transportation, and precipitation of calcium carbonate.

The soil solution of areas underlaid with caliche contained at one time considerable quantities of calcium bicarbonate, and probably still do. It was included, therefore, as a part of these investigations, to determine whether there is any marked relationship between the mineral content of the soils in different creosote bush areas and the variations in the osmotic values of the cell sap of the plants.

#### MATERIALS AND METHODS

Four areas were selected within a radius of twenty miles of the Desert Laboratory in which the dominant species in the plant association is the creosote bush. These areas were representative of the habitats, both good and poor, in which *Larrea* grows in the vicinity of Tucson.

At a representative location within each area a plot of approximately 100 square feet was staked out and all samples from each of the areas were taken from plants or soil within the limits of the respective squares. In fact, all of the leaf samples and weekly soil samples from any given plot were taken within a radius of thirty feet or less.

A description is given below of each of the four areas studied including a designation for each location which is intended to aid the reader in keeping in mind some of the features of the areas under discussion.

Area CB was so designated because it is located on the southern outwash slope or bajada of the Santa Catalina mountains three miles directly south from the entrance to Pima Canyon and about one and one-half miles north of the Rillito River. The creosote stand on this area is not as pure as those on the other three areas, being interspersed somewhat with *Carnegiea gigantea*, *Parkinsonia microphylla*, *Franseria deltoidea*, *Encelia farinosa*, a few small perennials and, in season, a few winter and summer annuals. However, within the particular plot chosen for study on this area neither of the large perennials *Carnegiea* nor *Parkinsonia* occurs and *Larrea* is by far the largest and the dominant plant. The soil is of granitic origin and "caliche" occurs at a depth of 12 to 24 inches below the surface. The creosote bushes here are 4 to 8 feet in height.

Area CP was selected primarily because the caliche or hardpan layer comes very close to the surface and is covered by only 6 to 12 inches of soil. In many places in the immediate vicinity large sheets of caliche are visible

at the surface. The caliche prominence lead to the selection of the designating letters "CP." This habitat is about 10 miles to the south and slightly east from area CB. Associated with *Larrea*, which is the dominant plant on this area, is a small herbaceous perennial *Crassina pumila* and a few winter and summer annuals which are active only during the rainy seasons. The bushes on this area have the poorest appearance and show the least amount of growth of those on any of the selected plots. They attain a height of only 3 to 4 feet; the older leaves are for the most part comparatively smaller; and a larger percentage of dead branches is present.

Area TB was so designated because of its geographical location on the westerly outwash slope or bajada of the Tucson mountains, 15 miles west of the Desert Laboratory. For all practical purposes this area represents a pure stand of *Larrea* at all seasons of the year. Only a few scattered representatives of *Echinocereus wislizeni* and *Opuntia spinosior* are present and only one each of these species was included in the plot selected for this work. The bushes on area TB show very good growth. They are more uniform in height, 4 to 5 feet, and in diameter than those of any of the other areas. The soil on this area is very deep and has been derived from the Tucson mountains, which are of volcanic origin. An excavation to a depth of 4 feet revealed no caliche layer and if a hardpan layer is present at a greater depth it is doubtful whether the *Larrea* roots come into contact with it.

Area LI or "Larrea Island" is the name applied by the author to an area in the Avra Valley approximately three acres in extent which is isolated from all other creosote areas, except for a smaller "island" 300 yards distant, by a very gently sloping grassland area 2 miles in extent along the shortest radius. Area LI is 5 miles indirectly west from TB. That this creosote "island" is a remnant of a more continuous stand is indicated by the fact that there is practically no reproduction on the area and there is no indication on the margin of the area that the *Larrea* is spreading. All of the bushes are relatively old, as indicated by their size, most of them having reached a height of 5 to 6 feet in most cases and having acquired a considerable quantity of dead branches. The soil on this area is probably of the same origin as that at area TB, although it is possible that some of it may have been brought in from greater distances. It has a greater sand content than soil from the other areas and an excavation to a depth of 4 feet revealed no caliche layer. This area is subject to light grazing and although stock do not eat mature *Larrea* it is quite possible that they may clip off the young seedlings along with other vegetation and, of course, some of the seedlings, if any start, may be trampled down. These factors, however, are not considered to be of sufficient magnitude to account for the almost total lack of new plants on the area. During the period of summer rains a very heavy covering of grass and summer annuals springs up on area LI and the surrounding grassland and



the winter rains bring numerous winter annuals into active growth. Except at these two periods of the year *Larrea* is the only active plant of importance on the area.

Within the plots staked out on each of the 4 creosote areas described above, two representative *Larrea tridentata* bushes were marked for study. The majority of the data obtained for the areas, by the methods used, center around these selected bushes. Beginning on March 8, 1931 and continuing at intervals until August 29, 1931, collections of leaves and adjacent small twigs were made from each of the eight chosen bushes and soil samples were taken at the same time for determinations of moisture content and total soluble salt content. The interval between collections varied from 6 to 17 days, depending upon the weather and other conditions. Most of the collections, however, were made at intervals of one week.

The methods followed in collecting and preparing the leaf material for the cryoscopic determinations and the method used in determining the osmotic values were in general the same as those reported by Walter (1931). Certain changes were found convenient and certain variations necessary to adapt them to studies of plants of the creosote bush type.

#### METHOD OF COLLECTING AND KILLING LEAF AND TWIG SAMPLES

The leaf and twig samples were collected in short glass vessels, test tube-like in shape, and closed by cork stoppers. The manner of taking the samples was to strip off the leaves and small twigs by grasping the foliage with the right hand and pulling upward and outward at proportionate intervals while slowly moving completely around the bush. One leaf sample was taken from each bush at each collection. The glass vessels were approximately one and one-half inches in diameter and had a capacity of approximately 75 milliliters. These were packed full of material, corked and then placed in a close-fitting aluminum canister which had a screw top.

The tissues were killed by placing the aluminum canisters containing the leaf samples in a vessel with moderately tight-fitting cover and by heating the material for 30 minutes in an atmosphere of boiling water. Water was placed about the sample cans up to one-third of their height and was brought to the boiling point as rapidly as possible. The entrance of water into the sample cans is readily detected by the presence of moisture in the soft dry tissue paper which is placed in the bottom of each aluminum canister. This small quantity of tissue paper also serves as a shock absorber for the glass vessel and serves to make the cork of the vessel fit tightly against the screw top of the canister, thus preventing the cork from being dislodged or loosened by pressure developed within the glass vessel during the heating. Following the heating process the samples were cooled to room temperature and then placed under refrigeration.

## METHOD OF EXTRACTING THE SAP

A Fred S. Carver hydraulic laboratory press was used for expressing the plant juices with a pressure of 14,000 pounds per square inch. This press gave very satisfactory results and was relatively easy and rapid to operate. The samples under refrigeration were allowed to come to room temperature before they were placed in the press. The material was then removed from the sampling jar with forceps and wrapped in a heavy muslin cloth about 15 centimeters square. The soiled cloths resulting from a series of pressings were boiled, rinsed, and dried before being used again.

Since there is no extraction chamber on the market suitable for expressing juices from biological material for cryoscopic determinations one was made from a good grade of stainless steel. This chamber differed somewhat from the press vessel described by Walter (1931) and the illustration, Figure 1.

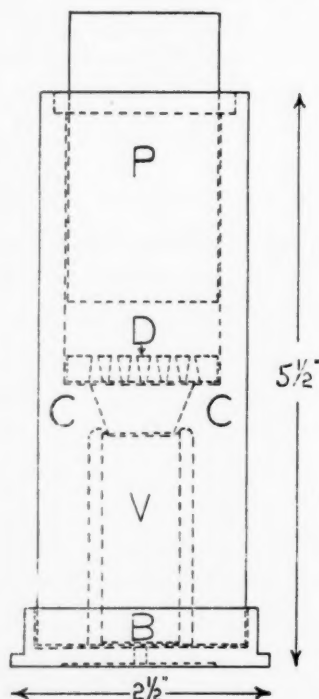


FIG. 1. Plant sap extraction chamber consisting of a main cylinder (C), a plunger (P), a perforated disc (D), a glass vial (V), and a brass base (B). Parts C, P, and D are of stainless steel.

shows the details of its construction. The addition of a groove cut around the inside wall of the main cylinder one inch from the top as described by Meyer (1929) would help prevent the upward movement of sap beyond that point. In this work the cell sap was squeezed directly into small vials in which it was stored until wanted for the cryoscopic determinations.

The order of assembling the extraction chamber is as follows: the per-

forated disc is placed in the bottom of the upper end of the main cylinder, a piece of clean muslin  $1\frac{1}{2}$  inches wide and 5 to 6 inches long is folded over two or three times and placed on top of the disc, the plant material wrapped in muslin as described above is then inserted in the upper end of the cylinder followed by the plunger. The insertion of the glass vial into the lower end of the cylinder and the mounting of the whole upon the brass base completes the operation. This assemblage is then placed upon the movable stage of the press and pressure is applied.

It was found quite essential to place two or three thicknesses of cloth over the perforated disc to prevent solid material from being pressed through. Although the osmotic value determinations would probably not be affected by the presence of solid materials in the sap, as shown by Hibbard and Harrington (1916) and others, the inconvenience and time consumed in cleaning the material out of the holes in the disc between each pressing warrants any precautions which can be taken to retain all of the solid material in the upper portion of the cylinder.

The use of such a high pressure as 14,000 pounds would not have been necessary during the rainy season but during the arid foreshummer it was quite difficult to obtain, even at that pressure, sufficient sap from a single collecting jar full of material to make a freezing point determination. When the material was quite dry the limit of its compressibility was quickly reached and the pressure indicator hand on the manometer remained stationary. As the material became more nearly saturated, with the advent of the rainy season, considerable time was required for the limit to be reached and since such a high initial pressure was being used it was thought unnecessary to continue the application of pressure until the indicator remained stationary, as would be advisable if a lower pressure were applied. Accordingly, a pressure of 14,000 pounds was applied and the extraction chamber was not removed from the press until either the pressure had dropped below 6,000 pounds, or, if the pressure did not decrease, until a period of 30 minutes had elapsed to permit the drainage of the sap into the vial. The vial containing the plant juice was removed from the cylinder, stoppered, and placed immediately in an electric refrigerator.

#### DETERMINATION OF THE FREEZING POINT

The majority of the cryoscopic work done in America has been accomplished with either a Beckmann or a Heidenhain thermometer. With these instruments it is necessary to have at least 15 milliliters of plant sap for a determination. When, however, a so-called microthermometer, such as a Drucker-Burian, is used, only 1.5 to 2 milliliters of juice is necessary. This feature is a distinct advantage in arid regions, especially when non-succulent plants are being studied. Also it is an advantage when numerous samples are to be collected from the same plant over a period of time, since only

relatively small amounts of material need be removed from the plant at any one time. Both of these factors were important in the present work and therefore a Drucker-Burian microthermometer, made by Robert Goetze, Leipzig, was used. Walter (1931) presents a good illustration and complete description of this equipment.

The expressed sap samples under refrigeration were allowed to come to room temperature before their freezing-point depressions were determined. The quantity of sap used must be sufficient to cover the thermometer to a height about 2 mm. above the mercury bulb.

After the freezing vessel and cell sap had been pre-cooled directly in the ice-salt mixture they were quickly transferred to the air jacket which had previously been suspended in the ice-brine mixture. The freezing vessel was held firmly in place in the air vessel by means of a cork gasket and care was exercised not to have the freezing vessel come into direct contact with the air vessel since this would lead to an unequal cooling of the sap. The solution to be tested was stirred constantly throughout the determination and the freezing mixture was also agitated from time to time.

When the desired degree of undercooling was attained a glass seeding capillary containing a particle of frozen distilled water was quickly introduced into the sap sample, immediately withdrawn, and the sap rapidly stirred. The seeding capillary may be successfully replaced by a length of platinum wire with a cork on the upper end to insulate against the heat of the hand. The highest point reached by the mercury is noted and for the first determination on a sample this reading was taken as the approximate freezing point, since the amount of undercooling was so great. This approximate value enables one to estimate very closely where the true freezing point will be and therefore the point at which the precooling should be stopped for an undercooling of one degree.

In the Drucker-Burian thermometer the scale is so short that it is impossible with most solutions to determine the total amount of undercooling which would occur if the solution were not disturbed, since the mercury would go below the scale. Therefore, it is necessary to stop the undercooling by seeding the solution with a crystal of ice as described above and the most convenient place to stop the undercooling is one degree centigrade below the actual freezing point, since this factor may then be disregarded in the correction formula which will be noted below.

Following the initial supercooling and freezing point determination the freezing tube is removed from the air jacket and the contents melted by holding in the hands and stirring gently. When all ice crystals have disappeared from the sample the freezing tube is again put directly into the ice-salt mixture for precooling. As soon as the mercury has fallen a little below the estimated freezing point the freezing vessel is transferred to the air jacket



for the remainder of the determination. At a temperature approximately  $0.3^{\circ}$  C. above the temperature at which the undercooling should be stopped, the solution is seeded with a crystal of ice. This anticipation of the undercooling temperature is necessary since the temperature invariably drops very suddenly about  $0.3^{\circ}$  C. immediately after the seeding and before it rises to the freezing point. In this work the process of determining the freezing point was repeated with each sample until two readings with a difference no greater than  $0.005^{\circ}$  C. were obtained.

It was found quite necessary to work at the same speed, in all determinations, especially in stirring. Otherwise the rapid rising and falling of the platinum stirrer will influence the temperature of the mercury filament unequally and inject error into the results. Considerable practice is necessary to acquire the proper technique and to obtain dependable results. The best indication of accurate work is the obtaining of two successive identical readings.

The determination of the zero point on the thermometer, which is the freezing point of distilled water, follows the same procedure as that given above for the plant sap.

#### CALCULATION OF THE OSMOTIC VALUE

The osmotic values are here reported in atmospheres of pressure. Variations in the osmotic values are more apparent when the values are expressed in atmospheres rather than in degrees of depression, since the units are larger. The correct values for depression of the freezing point were obtained by using the correction formula of Lewis (1908).

For converting the corrected depression of the freezing point readings into osmotic values expressed in atmospheres of pressure the tables of Harris and Gortner (1914) and Harris (1915) were used. Since according to Harris and Gortner, the first differences  $X_{0.1}$  may be taken as 0.012, the pressures when  $\Delta$  is read to thousandths of a degree may be readily determined. A detachable reading lens or a hand-lens is necessary for reading the thermometer to the third decimal point.

#### SOIL MOISTURE DETERMINATIONS AND RAINFALL RECORDS

The soil samples for the moisture determinations were collected in wide-mouthed, pint Mason jars at the same time that the leaf samples were taken and approximately one meter from the center of the crown of the bush. The jars were filled almost full and the moisture content was found on the basis of the percentage of the dry weight of the soil after it had been dried to constant weight at  $103$  to  $105^{\circ}$  C. Each sample consisted of approximately 360 to 700 grams of oven-dry soil. One sample was taken from the vicinity of each of the selected bushes on every leaf-collection tour, thus making a total of two samples from each area per collection.

Approximately 15 cm. was chosen as the most suitable depth at which to take the samples for two reasons; first, because on areas CB and CP it is impossible to dig much deeper without great labor, and second, because it was thought that samples taken at this depth would give a good indication of the moisture conditions with which young *Larrea* seedlings would come into contact and that they would give a better index to the fluctuations in the soil moisture than samples taken at shallower or at greater depths.

The rainfall records were obtained by means of rain gauges, one of which was placed on each area. These gauges were quite simple and consisted merely of a quart Mason jar, a one-hole cork stopper to fit the jar, and a large galvanized iron funnel. A quantity of a good grade of motor oil was placed in each jar to prevent the evaporation of the water between readings.

#### SOLUBLE SALT DETERMINATIONS

Periodic determinations of the total soluble salt content of the soils of the experimental areas were made in conjunction with the soil moisture determinations by means of the modified Wheatstone bridge as developed in the soil physics laboratory of the U. S. Bureau of Soils. A description of the electrolytic bridge and instructions for its proper manipulation have been published in convenient form by Davis (1927). He also gives tables from which the total soluble salts in solution at 60° F. may be read directly in parts per million for resistances from 68 ohms to 10,200 ohms.

#### MECHANICAL ANALYSIS OF SOILS

The hydrometer method of Bouyoucos (1928) was used in making the mechanical analyses of the soils from the respective areas. This method makes use of Stokes' law and hydrometer readings taken at given intervals of time. Bouyoucos found that the determinations made by his method agreed very closely with those obtained by the mechanical analysis method except in the case of the finer silt. Due to the fact that the finer silt has more of the characteristics of clay, the hydrometer method classes it with the clay while the mechanical analysis method places it with the coarse silt. For the type of work presented here the hydrometer method is sufficiently accurate, especially, since it is less complicated and requires less experience for proper manipulation than does the more time-consuming older method of mechanical analysis.

#### CHEMICAL ANALYSIS OF SOILS

The chemical analyses of soils from the four creosote areas and another area about 100 meters from LI on which no *Larrea* was present, were made in the agricultural chemistry department of the University of Arizona under the direction of Professor R. A. Greene. A 1 to 5 soil extract was prepared by shaking 100 grams of soil with 500 milliliters of water and filtering it

through a Pasteur-Chamberlin filter. The calcium and magnesium were determined by titration with standard soap solution and the chlorides by titration with standard silver nitrate. The amount of sulphates present was found turbidimetrically. Carbonates and bicarbonates were determined by titrating the soil extract with fiftieth normal sulphuric acid using phenolphthalein and methyl orange respectively as indicators. The quantity of sodium was calculated by the difference between the reacting values while the nitrates were determined colorometrically by the phenoldisulphonic method. These methods have been adapted or developed for use with southwestern soils by the agricultural chemistry department of the University of Arizona.

The soil samples for these analyses were all collected on the same day and each one was designed to be representative of the top six to eight inches of soil at the respective locations. Two samples were collected on each area, one from a high spot and one from a low place there being as much as one foot difference in elevation in some cases. A chemical analysis of the soil as described above was thought important in determining the uniformity or lack of uniformity between the *Larrea* habitats in respect to the chemical composition of the substrate.

#### ASH ANALYSIS OF PLANTS

The calcium and magnesium content of the plants growing on the various areas was determined in order to discover whether the presence or absence of caliche near the surface has any appreciable effect upon the amounts of calcium and magnesium absorbed by the plants. There is evidence that calcium compounds have strong imbibitional properties and that the drought resistance of a plant is at least partly dependent upon their formation, since they serve to bind water within the tissues. Also it was desired to determine whether any marked difference in the content of these two ions was reflected in the seasonal changes in the sap concentrations of the plants.

The plant material for these analyses consisted of root and top portions of ten plants from each area. The roots and tops were kept separate. The material was prepared for analysis according to the methods of the Association of Official Agricultural Chemists (1924 revision), page 39. For determining calcium the tentative volumetric method given in section 6, page 41 of the above publication was followed and the tentative gravimetric method for magnesium given in the succeeding section, number 7, page 42, was adopted up to the point where the sample is ignited and weighed as magnesium pyrophosphate. For the final determination of the magnesium the volumetric method of Handy as given in Scott (1917), was used.

#### DIURNAL VARIATIONS IN OSMOTIC VALUE

In order to determine what influence the time of collection of the leaf and twig samples might have on the osmotic values found for the various collec-

tions, samples were taken at two, three, and four-hour intervals, depending upon the time of day, for a period of fifty-two hours. Two *Larrea* bushes, A and B, located near the laboratory, were selected for this experiment. Bush A was a large one located in a pocket of soil surrounded by very large rocks which are thought to form a basin for moisture and to play an important rôle in its conservation, since this bush appeared to be in very good vegetative condition at all seasons of the year. Bush B was smaller than A but may be described as a representative bush. It was located on a well-drained slope about fifty yards from Bush A. The leaves of B were relatively small as compared to those of A but it too was considered to be in good vegetative vigor. Bush B was representative of the average creosote bush of the bajadas, judging from its general appearance, and bush A was representative of the large, tall, vigorous type of bush found in low spots where surface waters collect.

#### PRESENTATION AND DISCUSSION OF DATA

##### RELIABILITY OF THE METHOD OF SAMPLING

A short experiment was designed to determine the reliability of the method of taking the leaf samples as previously described. Four samples were collected from the same *Larrea* bush within a period of fifteen minutes. These samples were then treated in the manners described above and yielded the following values for the expressed saps:

Sample	$\Delta$	Ov
9x	1.965	23.620
10x	1.916	23.032
11x	1.896	22.796
12x	1.935	23.260

The greatest difference between these values is  $0.069^{\circ}$  C., or 0.832 atmospheres. This difference is somewhat greater than is desirable, however, since the values for samples 10 x, 11 x, and 12 x are relatively close together the greatest difference here being only  $0.039^{\circ}$  C. or 0.470 atmospheres, we may attribute the fact that sample 9 x gave such a high value, at least, in part, to some error in the determination rather than entirely to erratic sampling.

Two other instances may be cited in this connection. Duplicate leaf samples were collected in rapid succession from two *Larrea* bushes. One set of samples yielded osmotic values of 22.144 and 21.724 atmospheres and the other gave values of 28.340 and 27.990 atmospheres. From these data it is evident that differences in osmotic values of as much as 0.500 atmospheres may be accounted for as a variation in the uniformity of sampling when working with *Larrea* or a similar plant.



## SEASONAL VARIATIONS IN OSMOTIC VALUES

The variations in the osmotic values of the sap of leaves and small twigs of *Larrea tridentata* growing on the four experimental areas are presented in Figure 2. The average of the osmotic values found for each collection

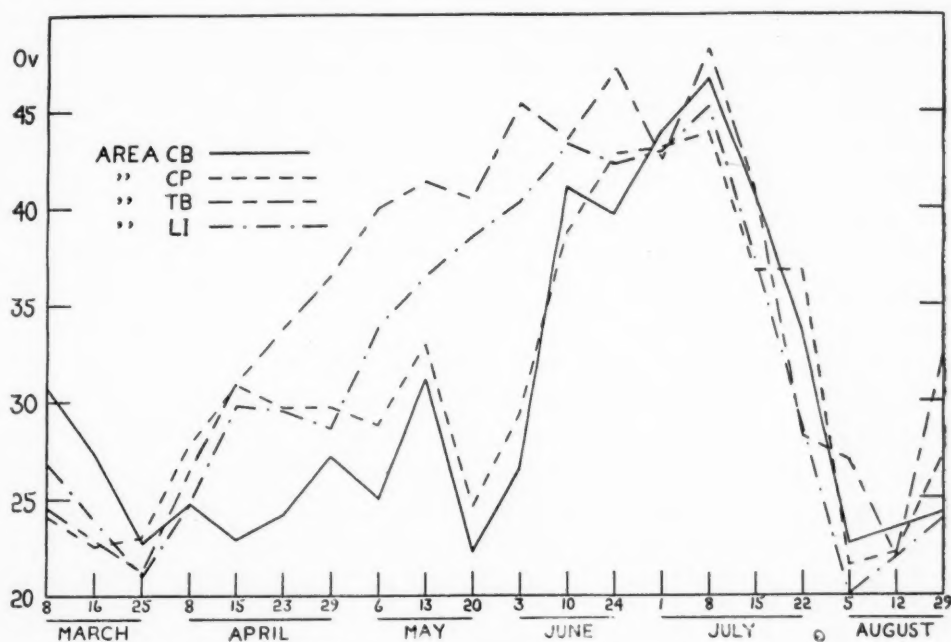


FIG. 2. Average osmotic values of the sap from leaves and small twigs of *Larrea tridentata*.

from two creosote bushes on each of the areas studied are used rather than the separate values found for all of the bushes. While it is not desirable to attempt to establish fundamental facts upon studies of such a limited number of individuals, numerous determinations on the same individuals over a considerable period of time serve to offset this weakness. Moreover, on two occasions during the course of these studies samples were collected from a considerable number of individuals on each area for the purpose of determining the individual variations in the osmotic values on each area at a given time. The results of these tests will be reported later in this paper.

Figure 2 reveals several facts concerning the seasonal variations in the osmotic values of the creosote bush. The highest average osmotic values for all four of the areas were found for the collections of July 8th. The lowest average osmotic values for areas CB and TB occurred on March 25th and the lowest values for CP and LI on August 5th. Moreover, on March 25th, July 1st and August 12th the osmotic values for all four areas were closer together than at any other time during the season. These facts indicate therefore that the greatest response of these plants to environmental conditions as indicated by changes in the concentration of the cell sap takes place

in approximately the same length of time regardless of variations in the environmental factors during the period between the occurrence of maximum and minimum sap concentrations. Also it will be noticed that the osmotic values become more nearly equal as the maximum and minimum values are approached. This is due mainly to the fact that as the limits of desiccation or saturation are reached the effect exerted on the concentration of the sap by the volume and activity of the root system is minimized.

The minimum osmotic values are more nearly equal for all areas than are the maximum values. This may be taken as an indication that the qualities of a creosote bush which make for drought resistance are not present in equal degrees in the plants on the different areas. If the degree of drought resistance is chiefly dependent upon the quantity of hydrophilic colloids or other substances which may bind water within the plant, then plants which contain different quantities of such substances will possess different osmotic values, especially as the tissues become drier and drier.

The sap concentrations of leaf and twig material collected on areas CB and CP were more constant than those from areas TB and LI. From the locations of the areas given above it will be recalled that areas CB and CP and areas TB and LI are much closer to each other geographically than they are to any of the other areas. Therefore, the environmental factors affecting the plants of these two pairs of creosote areas would be expected to be and, as will be shown later, are more nearly equal than those for any other combination of locations studied. This also explains the closer equality of values from areas CB and CP and from areas TB and LI throughout the season than from any other two areas.

The curves for all of the *Larrea* areas, produced by plotting their osmotic values on the same scale, are quite similar. In general, they resemble the "normal distribution" curve. The curves for TB and LI rise more gradually than those for CB and CP, probably due to differences in the climatic factors, but the curves all descend together and somewhat more abruptly than they rose, as the summer rainy season advances.

A summary of the seasonal range of osmotic values for the individual creosote bushes and the individual areas studied is given in Table 1 for the period March 8 to August 29, 1931.

TABLE 1. Seasonal range of osmotic values arranged in descending order.

Individual Bushes	Max. Ov.	Min. Ov.	Range of Variation
TB <sub>5</sub>	50.472	21.376	29.096 atm.
LI <sub>7</sub>	48.644	20.368	28.276 "
TB <sub>0</sub>	49.006	21.016	27.990 "
CB <sub>1</sub>	47.262	22.192	25.070 "
CB <sub>2</sub>	46.456	21.484	24.972 "
CP <sub>3</sub>	45.784	22.240	23.544 "
LI <sub>8</sub>	42.082	19.828	22.254 "
CP <sub>4</sub>	42.646	20.656	21.990 "
Average	46.544	21.145	25.399

Individual Areas	Max. Ov.	Min. Ov.	Range of Variation
TB	48.422	21.196	27.226
LI	45.363	20.098	25.265
CB	46.859	22.408	24.451
CP	44.155	21.664	22.491

Except in the case of bushes  $LI_7$  and  $LI_8$  the bushes from the areas form a very regular series with the succession  $TB_5$ ,  $TB_6$ ,  $CB_1$ ,  $CB_2$ ,  $CP_3$  and  $CP_4$  when they are arranged in the descending order of the range of variation of their osmotic values. This affords evidence that there is a fairly characteristic range of osmotic values for this plant for each particular habitat in which it grows and that this range is practically the same for all *Larrea* plants growing in any given habitat. Bush  $LI_8$  is the only one studied which does not fall in line with this evidence. However, in spite of the fact that its range is next to the lowest in the series, yet area LI is able to hold second highest place in the seasonal range of osmotic values because the seasonal range for bush  $LI_7$  was sufficiently large to keep the average up. The great difference between the values for  $LI_7$  and  $LI_8$  are not surprising. As stated above, the creosote plants on the "Larrea Island" are apparently merely holding their own against fatally adverse conditions. It is to be expected, therefore, that the principle of the survival of the fittest will be most operative in this habitat and that the individual differences between plants will be more apparent than they would be under more favorable conditions of growth.

The arrangement of the four areas in a series in the descending order of their seasonal range of osmotic values corresponds exactly to a classification of the areas based on the desirability of the habitats for the growth of creosote as indicated by the appearance of the bushes and the amount of vegetative growth and reproduction present. Starting with the best habitat and ending with the poorest, the classification of the areas would be TB, LI, CB, and CP. These facts would lead one to believe that a wide range of variation in osmotic value is favorable to the plant but it may be argued that since the greatest differences are in the maximum values, the conditions of drought did not become equally severe on all of the areas, and had the dry period continued for a greater length of time, the ranges of variation would have been closer together, if not equal. The writer judges, however, that a continuation of climatic conditions which would raise the maximum osmotic value of one bush would also increase that value of the plants on all of the areas, and in order for all of the bushes to reach the same maximum value a difference in rate of change or a difference in the "osmotic inertia" of *Larrea* such as suggested by Walter (1929) for plants of different species, would have to be operative. The curves in Figure 2 do not give support to this theory when it is applied to plants of *Larrea*, since during the periods when conditions were more nearly uniform on all of the areas, the osmotic values quickly approached each other and the response was quite uniform as long as conditions remained approximately equal.

The osmotic values reported by Whitfield (1932), for *Artemisia californica* appear to support the observation that plants of a given species which experience the widest range of osmotic values also exhibit the best growth. Plants of this species from the sand dunes where its growth is best had a range of 11.2 atmospheres, those from the coastal chaparral 3.8 atmospheres, and specimens from the coastal sagebrush associations 0.8 atmospheres. Samples were collected at only two seasons and it is possible that the extreme values were not obtained. The limited data are in line, however, with the findings for the creosote bush.

OSMOTIC VALUES OF LARREA AS INFLUENCED BY SOIL MOISTURE  
AND RAINFALL

In Figures 3 and 4 a graphic comparison is presented of the percentages of soil moisture with the osmotic values and with the precipitation in inches. The total rainfall on the different areas during the period of the investigation

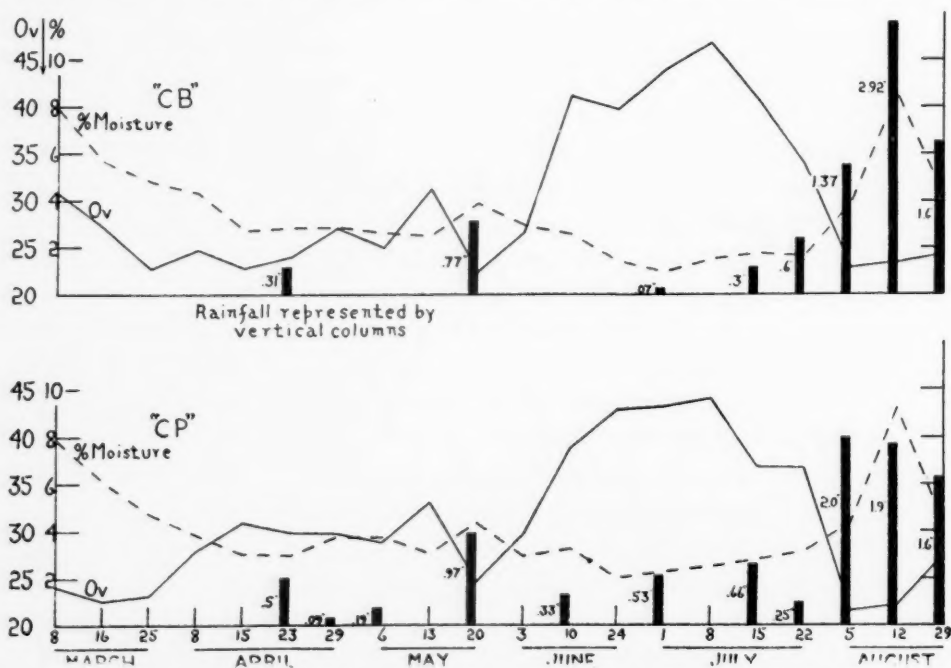


FIG. 3. Osmotic values of *Larrea* on areas CB (above) and CP (below) in relation to soil moisture and rainfall. Total rainfall between readings is indicated in inches by the figures adjacent to the black columns.

was as follows: CB, 8.00 inches; CP, 9.04 inches; TB, 6.71 inches; and LI, 6.70 inches. The distribution of this precipitation is shown by the location of the vertical columns on the graphs. From the position and height of these columns it is apparent that the rainfall pattern for all four areas was quite similar. Area CP, which received the most rain, had precipitation during three periods when the other areas received none. This indicates that



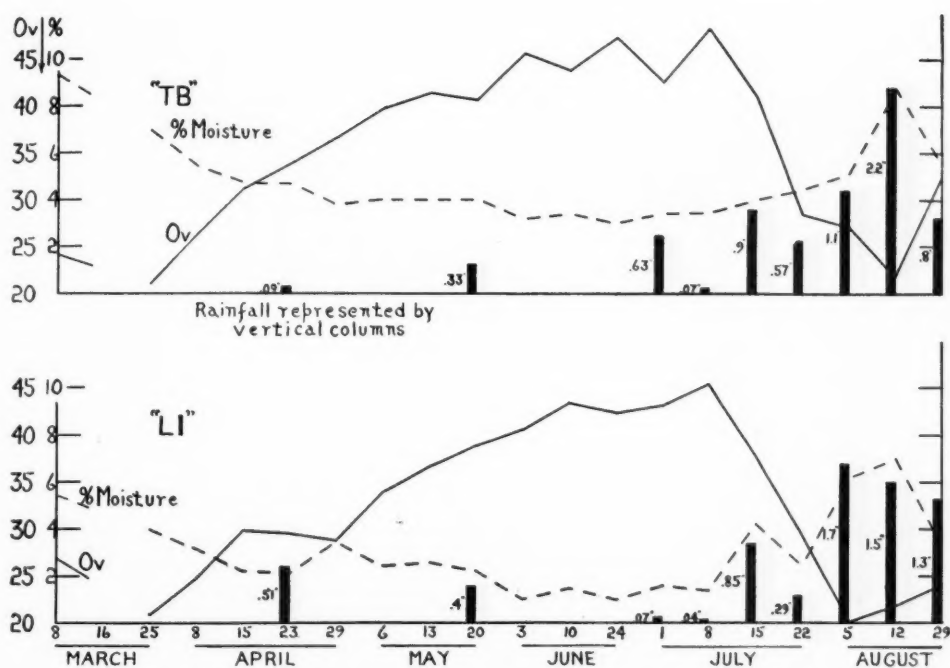


FIG. 4. Osmotic values of *Larrea* on areas TB (above) and LI (below) in relation to soil moisture and rainfall. Total rainfall between readings is indicated in inches by the figures adjacent to the black columns.

the larger total for this area may be attributed to a greater number of separate showers rather than to heavier rainfall on the same days in which all of the areas received moisture. Only one of these three periods; namely, that from June 3 to June 10 yielded sufficient moisture to be of much aid or importance to the vegetation. The precipitation for this interval was 0.33 inch while for the other two periods it was only 0.09 and 0.19 inch. The fact that area CP received rain over a greater period of time may have been one factor in preventing the Ov from rising as early or as high as those for areas TB and LI; however, it is interesting to note that the fall of 0.33 inch of rain on area CP did not prevent the osmotic concentration from beginning its rise toward the seasonal peak on the same day as it did for area CB although the sap concentration did not increase quite as much as it did for CB. It seems, therefore, that factors other than rainfall alone were influencing the change in osmotic value.

The season of summer rains may be considered as beginning on July 1st for areas CP and TB but not until July 15th for areas CB and LI. All of the osmotic values, however, show a relatively equal decrease on the same day, July 8th, regardless of the amount of precipitation. This again indicates that some other factor was more important than the amount of rainfall.

Turning now to a consideration of the percentage of soil moisture at a depth of approximately 15 centimeters, in the various habitats throughout

the season, a close correlation is seen to exist between it and the osmotic value of the expressed sap of leaves and twigs of *Larrea*. An increase in the moisture content produced a decrease in the osmotic value in practically every instance, especially if the change in soil moisture content was as much as 0.25 per cent. The average of the moisture contents of the soil in the respective areas, as determined at intervals during the period of this investigation, was 3.5 per cent for CB, 4.0 per cent for CP, 4.7 per cent for TB and 3.0 per cent for LI. The low value for LI is probably partly attributable to the fact that the soil of this area contained a larger percentage of sand than did any of the other soils and therefore its water-holding capacity was less and the moisture evaporated more readily from the first few inches and also penetrated deeper than on the other areas. The moisture content of soil samples taken at about 25 centimeters on area LI would probably have been more nearly equal to the moisture content of the 15 centimeter samples from the other areas. Nevertheless, area TB which had the highest seasonal average moisture content of the soil also has a soil which is quite sandy, as was shown by the results of the mechanical analysis. Regardless of the fact that area TB had the highest average percentage moisture and area LI the lowest, yet the sap concentration of both of these areas began to rise toward the seasonal peak on the same day, March 25th, and suffered only minor decreases until the maximum osmotic value for the season was reached. On the other hand, areas CB and CP did not show a definite continuous rise toward the maximum concentration of the sap of leaves and twigs of *Larrea* growing on them until May 20th. Then the plant sap from both areas exhibited a definite increase toward the seasonal peak of osmotic values. Soil samples from areas CB and CP yielded average percentage moisture contents for the season which are intermediate when compared with the corresponding values found for the other two habitats. The writer believes that differences in response were not due primarily to differences in rainfall on the areas or to basic differences within the plants on the four areas but rather to the presence of the layer or layers of caliche in the soil of areas CB and CP which served to prevent rapid movement and evaporation of moisture which had penetrated through cracks and crevices to the soil beneath the caliche. The roots of the plants on these areas had also penetrated the caliche more or less successfully and were drawing upon the moisture of the soil beneath, thus prolonging the period of low sap concentration eight weeks over that of areas TB and LI. It is true that areas CB and CP received more moisture from the rains which fell about April 23rd and May 20th than did either of the other two habitats. But, in view of the fact that the sap concentrations began to rise immediately following the precipitation of over 1.5 inches around May 20th, these rains evidently had little effect on the vegetation and it was the moisture conserved by the caliche which was the chief factor in keeping the osmotic values low, up to and including that time.

It is interesting to note that the highest osmotic concentration for each of the areas occurred at least one week, and in most cases, two weeks after the lowest moisture content of the soil at a depth of 15 centimeters. This lag is to be expected since the soil at 15 centimeters dries out much more rapidly than does the soil which surrounds the bulk of the root system at greater depths. However, the "osmotic inertia," of the plants may also be a factor here, and if so, it is evident that the rate of change is approximately equal on all areas.

Except in the case of area TB the lowest sap concentrations were found in the samples collected one week before the highest percentage soil moisture occurred. If we eliminate the determinations of soil moisture for area TB for the period prior to April 8th which is, moreover, not complete, then the highest soil moisture for all of the areas occurred on the same day, August 12th, which was in the midst of the summer rainy season. The weather during the period between August 5th and August 12th, was wet and cloudy and therefore the top soil did not have an opportunity to dry out as it had previously and besides it was becoming saturated. This accounts for the high moisture content on this day at 15 centimeters. The plants had received sufficient moisture by August 5th to produce the lowest sap concentration except in the case of those bushes on area TB, where, however, the lowest osmotic value was found on August 12th. This again emphasizes the fact that the response of the plants on all of the areas to soil moisture is, for all practical purposes, equal when the response is measured in terms of osmotic value.

While the number of determinations of the moisture equivalent and wilting coefficient of these soils is very limited it is reported here because it proved to be very interesting and to have a significant bearing upon the moisture relations of Larrea. The method of Briggs and McLane (1907) was used in making the moisture equivalent determinations. The average moisture equivalents of two determinations for each area in per cent were as follows: CB, 11.09; CP, 12.71; TB, 15.74; and LI, 8.75. The formula of Briggs and Shantz (1912) was used for calculating the wilting coefficient from the moisture equivalent for the respective soils. The wilting coefficients in per cent are as follows: CB, 6.03; CP, 6.91; TB, 8.55; and LI, 4.75.

Comparing these calculated wilting coefficients with the average soil moisture determinations an interesting fact is brought to light. In only two collections of soil from CB, CP, and TB and in three collections from area LI did the percentage of soil moisture exceed the wilting coefficients for the respective soils. These samples were taken on March 8th and August 12th for all the areas and also on August 5th for area LI. The soils collected on all other dates during the period of this investigation contained a percentage of moisture below the wilting coefficient. In the case of area TB this deficit

amounted to 5.5 per cent on June 24th. All of the maximum deficits occurred on the same date for all areas except CB, where it occurred one week later.

That *Larrea* can survive under these conditions is self evident. In fact, the area (TB), on which the creosote bush was conceded to be making the most successful growth, showed the greatest moisture deficit at 15 centimeters. What the moisture conditions were below this depth are not known. Breazeale (1930) has determined experimentally that some plants may absorb moisture from any soil horizon where water is available, for example, a subsoil, and transport this moisture to another horizon, where moisture is scarce, for example, the surface soil. Here the plant may "exude" this water; the water may in turn dissolve and absorb certain amounts of nutrient material. He used wheat and corn in his experiments. Considerable research will be necessary to determine whether this holds for *Larrea*. That *Larrea* must produce root hairs in the upper layers of soil which are either active all the time or are quickly brought into an active state is indicated by the ready response of the creosote bush to rains which penetrate the soil to a depth of only two to four inches.

Another interesting consideration connected with the above data is the relationship which the moisture content of the upper layer of soil may bear to reproduction of *Larrea*. It is difficult to understand how young seedlings can become established in soil which, during a very great part of the time, has a moisture content below the calculated wilting coefficient for that soil. Magistad and Breazeale (1929) have pointed out that roots of cactus (*Opuntia*) will grow into soil, and will live and elongate in soil in which the moisture content is kept at the wilting percentage or even in an air-dry condition. The plant will continue to live under such conditions only so long as it contains sufficient moisture to meet its metabolic needs and to keep the moisture content of the soil atmosphere immediately surrounding the roots in equilibrium with the moisture content of the roots. It is known that cactus joints are readily rooted by placing them in air-dry soil or sand and allowing them to stand without water until the root system is established. The soil in such cases serves primarily as an insulation against the rapid diffusion of the water vapor given off from the underground parts of the plants. The resulting increase in the humidity of the atmosphere of the soil stimulates the growth processes of the plant and roots are produced. These facts are readily understood for plants or plant parts which possess large water-storing capacities. However, such facts have not been established for seedlings of these plants or for a non-succulent, woody perennial like *Larrea*. In general it may be stated that plants, especially mesophytes, cannot reduce the moisture content of soil below the calculated wilting percentage except, perhaps, under conditions where there is a sufficient water supply in the lower levels of soil and where enough roots penetrate therein to furnish the bulk of the water necessary to replace that lost from the leaves.



The possibility is great, therefore, that the low moisture content of the upper layers of soil may play an important rôle in bringing about the scanty reproduction of the creosote bush. A typical creosote area is not densely populated by *Larrea* and usually the surface of the soil is relatively free from vegetation. The first 30 cm. of soil is quite well permeated by roots and there is no doubt some competition for moisture. However, there cannot be much competition in soil in which the moisture content is below the wilting percentage nearly all of the time. It seems probable, therefore, that seedlings of *Larrea* are able to survive in soil in which the moisture content is below the calculated wilting coefficient and is also below the percentage at which many plants would permanently wilt. If this is not true, then new creosote bushes become established only during periods in which the rainy season is sufficiently extensive and intensive to raise the moisture content of the soil above the wilting percentage long enough to give the seedling roots an opportunity to become established at a depth where the moisture content is adequate throughout the year. The greatest number of young creosote bushes per given unit area are almost invariably found where the soil has been disturbed as, for example, along roadways and around excavations where scrapers and other implements have loosened and piled up the soil. This indicates that seed germination and seedling development are aided or are made possible by covering the seeds to prevent rapid desiccation and by loosening the soil to facilitate the penetration of the roots. Moisture also penetrates more readily into soil which has been disturbed and there is less lost as "runoff." The rain that falls is therefore more effective in maintaining the moisture content of the soil.

OSMOTIC VALUES OF *LARREA* IN RELATION TO THE TOTAL SOLUBLE  
SALT CONTENT OF THE SOIL

As would be expected, there is apparently no correlation between the total soluble salt content of the soil at 15 centimeters and the osmotic value of the sap of leaves and twigs of *Larrea* growing thereon. The greatest variation in the determinations was found on area TB where it amounted to 115 parts per million; a change of only 0.0115 per cent. This amount of change is not of sufficient magnitude to be of any importance to the life of the plant coming into contact with the soil solution. The variation at greater depths in the region of the main bulk of the roots was probably even less than at 15 centimeters where the salts are more subject to leaching.

The seasonal average soluble salt concentration in parts per million for the soils of the various habitats were 206 for TB, 145 for CB, 139 for CP, and 102 for LI. The difference between the highest and lowest of these values, 104 p.p.m., might be important in connection with reproduction since it is the salt concentration at a depth of around 15 cm. with which the young seedlings first come in contact. An area with a relatively low salt concen-

tration would be most favorable for young plants. However, if the areas are arranged in the descending order as regards the presence of young plants on them, they would be in the same order as when arranged in a series of decreasing soluble salt content; namely, TB, CB, CP, and LI.

Total soluble salt determinations made on the same soils in the agricultural chemistry department of the University of Arizona were considerably higher than those made with the "soil bridge." The values obtained at the chemistry department were for TB, 292 p.p.m.; for CP, 287 p.p.m.; for LI, 278 p.p.m.; and for CB, 248 p.p.m. These concentrations are practically equal since there was only 44 p.p.m. difference between the highest and the lowest values. Two samples taken about 100 meters from LI, where no creosote was growing, gave values of 155 and 269 p.p.m. or an average of 212 p.p.m. This average is lower than the lowest concentration of soluble salts found by the same method for the *Larrea* areas, although it is doubtful whether the difference is great enough to have any appreciable bearing on the absence of creosote on this area.

#### SUMMARY OF SEASONAL VALUES

As an aid in comparing and visualizing the condition of osmotic value, soil moisture content, precipitation, and total soluble salt concentration existing on the various areas, a summary of seasonal or average values for the duration of this investigation is given in Table 2. These values show that area TB with the highest average moisture content and the highest average salt content also displayed the highest average osmotic value for sap of *Larrea*. This relationship did not hold for area LI which was characterized by the lowest average moisture content and soluble salt content, and likewise by the lowest total rainfall; yet the plants of this area gave the second highest value.

TABLE 2. Summary of seasonal values.

Type of Data	CB	CP	TB	LI	Arranged in descending order of values
Seasonal Average Osmotic Value per Collection.....	30.125 atms.	30.906 atms.	35.475	32.490	TB-LI-CP-CB
Seasonal Average % Soil Moisture.....	3.5%	4.0%	4.7%	3.0%	TB-CP-CB-LI
Total Seasonal rainfall.	8 in.	9 in.	6.71 in.	6.70 in.	CP-CB-TB-LI
Seasonal Average Soluble Salt Content of Soils.....	145 p.p.m.	139 p.p.m.	206 p.p.m.	102 p.p.m.	TB-CB-CP-LI

## MECHANICAL ANALYSIS OF SOILS

The results of the mechanical analysis of the soil from the four creosote areas as determined by the hydrometer method of Bouyoucos are presented in Table 3. The classification of the soils is based on a diagram by Lyon and Buckman (1922). These figures show that the soil on area LI contains considerably more sand than does soil from any of the other areas. Therefore, its water holding capacity is less and it is subject to more rapid drying out than the other soils. This helps to explain the scarcity of reproduction on this area, since the soil may dry out so rapidly between rains that the young seedlings cannot become established well enough to survive the drought.

TABLE 3. Mechanical Analysis of Soils.

Area	Sample	Per Cent Sand	Per Cent Silt	Per Cent Clay	Classification
CB	1	74.36	12.0	13.64	Sandy loam
CB	2	72.87	10.8	16.33	Sandy loam
CP	3	72.47	13.0	14.53	Sandy loam
CP	4	66.57	13.5	19.93	Sandy loam
TB	5	57.50	14.0	28.50	Sandy clay
TB	6	62.15	12.5	25.35	Sandy clay
LI	7	85.36	5.5	9.14	Sand
LI	8	76.50	8.5	15.50	Sandy loam

## CHEMICAL ANALYSIS OF SOILS FOR ALKALI SALT CONTENT

A chemical analysis of the soil from each of the four *Larrea* areas showed that there was very little difference between them in respect to chemical composition of the top 5 to 8 inches of soil, from which the samples were taken. Areas CB, CP, and TB were remarkably uniform in sodium, calcium, magnesium, chloride, bicarbonate, and nitrate content. Area LI was very similar to these except in the case of calcium, of which it contained none, and of sodium, of which it contained 20 p.p.m. more than the other areas.

The average values in parts per million for two chemical analyses for each area are presented in Table 4. In the last column the average pH value of four determinations on each soil are given.

TABLE 4. Chemical Analyses and pH of Soils.

Area	Na	Ca	Mg	Chlorides	Bicarbonates	Nitrates	pH
CB	41	15	12	10	183	11	7.62
CP	40	15	15	10	195	12	7.57
TB	41	15	15	10	201	10	7.74
LI	60	0	12	10	188	8	7.55

ASH ANALYSIS OF *Larrea tridentata*

The ash of the tops and roots of portions of ten *Larrea* plants from each area were analyzed for the calcium and magnesium content, in order to determine whether or not the presence or absence of caliche had any apparent relation to the amounts of these elements absorbed by the plants or whether there was any connection between the calcium and magnesium content and the variations in the sap concentrations of the plants. The results of these analyses are presented in Table 5.

TABLE 5. Calcium and Magnesium Content of *Larrea tridentata*.\*

Area	Tops			Roots		
	CaO	MgO	Ratio Ca/Mg	CaO	MgO	Ratio Ca/Mg
	<i>Per Cent</i>	<i>Per Cent</i>		<i>Per Cent</i>	<i>Per Cent</i>	
CB	22.45	6.122	3.67	17.120	4.603	3.72
CP	16.86	4.775	3.66	8.069	3.004	2.67
TB	15.43	4.795	3.22	12.660	4.048	3.13
LI	24.90	6.285	3.96	7.251	2.292	3.16

\*Percentages based on oven dry weight of ash used.

In both tops and roots the percentage of calcium oxide is greater than the percentage of magnesium oxide in every case. This is to be expected, since such a relationship holds in general for all plants. The presence of caliche near the surface apparently does not affect the absorption of calcium by *Larrea*, since the tops of plants growing on areas TB and LI, where caliche was either absent or more than four feet below the surface, contained respectively both the lowest and the highest percentage found. Although the chemical analysis of soil from LI showed no calcium present in the first eight inches, the soil at greater depths must contain as much as the other areas, since the tops of plants from this area yielded the highest percentage of calcium oxide.

Differences existing between the plants from the different areas in respect to the percentages of calcium oxide and magnesium oxide which they contain or the calcium-magnesium ratios do not correlate with differences in the range or with changes in the osmotic values of the sap of leaves and twigs from plants growing on the areas. The hydrogen ion concentrations of the soil solutions of the four soils from the selected areas as determined with the quinhydrone electrode were practically equal. The greatest difference in pH was 0.19, most of which difference could be accounted for as experimental error since considerable "creeping" of the potential occurred during the measurements. This "creeping" as reported by McGeorge (1929) was probably due to the presence of manganese in the soil.

#### DIURNAL CHANGES IN THE OSMOTIC VALUE AND MOISTURE CONTENT OF THE LEAVES AND SMALL TWIGS

The variations in moisture content and osmotic value of the leaves and twigs were quite regular throughout the 53 hour period during which the samples for this experiment were collected.<sup>3</sup> As will be seen from Figure 5 the maximum sap concentration for bush A came at 3 p.m. on both days while the maximum for bush B was found at 1 p.m. on both days. This lag on the part of bush A was probably due to two factors; first, bush

<sup>3</sup> The writer is indebted to Mr. E. H. Runyon for determinations of the moisture content.



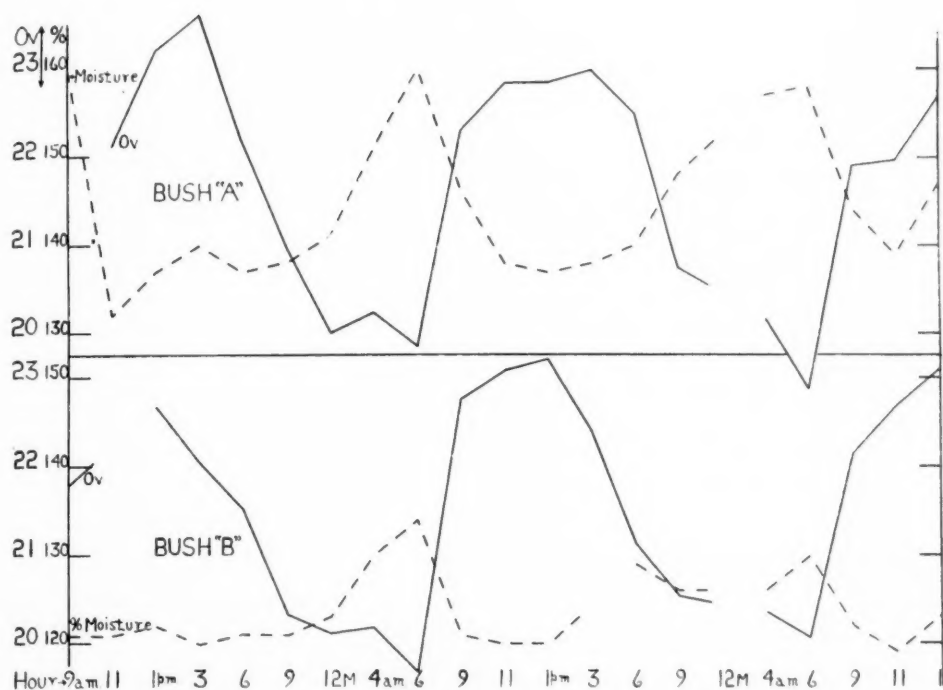


FIG. 5. Diurnal variations in osmotic value and moisture content of leaves and twigs of *Larrea*. Data for bush A above, for bush B below. Prolonged breaks in the graph lines indicate no determinations for those dates.

A was considerably larger than B and therefore had a larger and more extensive root system to absorb moisture and, second, and no doubt more important than the first, bush A was growing in a pocket of soil surrounded by large rocks which form a basin and therefore the moisture content of the soil in contact with the roots was probably much greater than that around the roots of B, which was situated on an open, well-drained slope. These contentions are supported by the fact that the moisture content increased considerably more in A than in B during the night. Herrick (1933) found that the osmotic and suction tension values of *Ambrosia trifida* also reached their maximums between 1 and 3 p.m. daily.

The lowest osmotic values for the two bushes were found in the 6 a.m. collections from both bushes on both days. The rapid increase in osmotic concentration in the 3- to 5-hour period beginning around 6 p.m. is largely due to rapid transpiration. However, the increase in the photosynthetic rate and subsequent accumulation of the products of photosynthesis no doubt serves to increase the concentration of the cell sap also. The decrease in osmotic value which begins about 3 p.m. for bush A and 1 p.m. for bush B was accompanied by an increase in moisture content. This indicates that the rate of transpiration is checked at those times and that the moisture content is of greater importance than the photosynthetic rate in determining the concentration of the plant sap. Bush A with a greater range of osmotic concen-

tration (3.7 atmospheres) also had the greater variation in its moisture content (28 per cent). The soil moisture at 15 centimeters was about 1 per cent higher at B than at A. However, this difference is not very significant since owing to the location of A among very large rocks it was difficult to obtain a representative soil sample even at that shallow depth.

These results show that the time of day is important when samples for cryoscopic determinations or moisture content are being collected. All of the samples for a comparative study should be collected at as nearly the same time of day as possible. The least change occurs during the period from 11 a.m. to 1 p.m. and from 4 a.m. to 6 a.m. Collections made between 6 and 9 a.m. may vary as much as 3.7 atmospheres due to difference in time of collection alone.

#### INDIVIDUAL DIFFERENCES IN OSMOTIC VALUE BETWEEN LARREA BUSHES IN THE SAME HABITAT

Near the peak of the arid foresummer, July 1st, ten samples of leaves and small twigs were collected on each area from ten different plants to determine how much difference in osmotic concentration existed between plants in the same habitat at a given time. The water deficit of the plants was so high at the time of collection that, as may be seen from Table 6, only a few of the samples from two of the areas yielded sufficient sap for a determination. Because of this failure to get enough juice from the tissues one-half of the experiment was repeated near the peak of the rainy season, August 8th, at which time all of the 8 samples collected on areas CB and CP yielded much more than the required quantity of sap. The values found for these samples, the average osmotic values, the differences between the highest and lowest osmotic values, and the greatest deviation from the mean osmotic value in each case are included in Table 6.

The results show that differences of over 8 atmospheres may exist in different bushes on the same area at a given time during periods of drought. During rainy periods, however, the differences tend to be somewhat less. In studies of this nature, as the above data indicate, it is better, where the size of the plant permits, to take the average of complete samples from individual plants when establishing the average osmotic value for a given species in a certain habitat rather than composite samples from a large number of individuals. And when one wishes to follow the changes in the osmotic value from time to time it is highly important that the samples be collected from the same bushes and in as nearly the same manner as possible each time.

#### GENERAL DISCUSSION

Of the conditions of the environment studied in this investigation soil moisture and rainfall apparently exert the strongest influence upon the variations in the osmotic value of the cell sap of the leaves and small twigs of

TABLE 6. Osmotic value differences between plants.

Sample	JULY 1ST				AUGUST 8TH	
	CB	CP	TB	LI	CB	CP
1.....	45.338	45.784	43.140	47.070	22.432	23.632
2.....	42.874	40.700	42.034	39.198	22.912	27.342
3.....	50.364	n. s. s.	42.202	43.728	24.568	24.040
4.....	n. s. s.	40.122	42.358	n. s. s.	23.500	26.094
5.....	46.746	n. s. s.	n. s. s.	n. s. s.	23.620	24.738
6.....	43.464	n. s. s.	34.910	n. s. s.	23.980	26.694
7.....	45.074	n. s. s.	n. s. s.	n. s. s.	22.144	28.340
8.....	n. s. s.	n. s. s.	41.672	42.166	21.724	27.990
9.....	43.692	n. s. s.	37.156	n. s. s.	.....	.....
10.....	47.166	41.758	36.038	n. s. s.	.....	.....
Average Ov. ....	45.590	42.091	39.951	43.040	23.110	26.045
Difference between highest and lowest osmotic values. ....	7.490	5.662	8.230	7.872	2.844	4.708
Greatest deviation from the mean Ov. .	4.774	3.693	5.041	4.030	1.458	2.413

\*n. s. s. indicates that there was "not sufficient sap" obtained from the sample for a determination.

*Larrea tridentata*. This is to be expected, especially in a semi-arid region, and it is in accord with the findings of Korstian (1924) for plants in the Wasatch mountains of Utah. That he did not discount entirely the effectiveness of other factors is shown by the following statement: "The concentration of the sap of a species is not constant. It may be influenced by any of the environmental conditions affecting transpiration, the products of photosynthesis, or the supply of available soil moisture. Osmotic pressure in plants is more rapidly changed by fluctuations in the moisture conditions of the site than by temperature or light."

Differences in light intensity, temperature, and wind movement were not taken into account in this work since it is believed that they are very slight for the creosote areas studied. Spalding (1904) has shown that the transpiration rate of *Larrea* is governed by the supply of available moisture in the soil; the more water present, the higher the rate of transpiration.

That light is an important factor influencing the osmotic pressure of plant saps has been shown by several workers. Dixon (1910) noted that illumination increased the osmotic value in leaves while darkness decreased it. This he attributed to increases in the soluble carbohydrates in light. Chandler (1913) found that shading plants such as corn and Canada field peas 24 hours caused a decrease in the sap densities. In a study of the osmotic values of the cell sap of the leaves of certain evergreen trees Gail (1926) attributed fluctuations in the values during February and March to the effect of cloudy

days alternating with days of sunshine. Continuous cloudy weather caused a lowering of the osmotic pressure, owing to a decrease in the photosynthetic rate. These observations suggest that variations in light intensity and the accompanying variations in the rate of photosynthesis may be responsible for the fact that the osmotic value of the expressed sap of leaves and twigs of *Larrea* did not respond as quickly or as greatly at all times to a given change in the moisture content of the soil. A hard rain of short duration preceded and followed by periods of considerable sunshine might not affect as great a change in the osmotic values as would follow if the precipitation occurred during an extended period of rather cloudy weather, since the products of photosynthesis would then continue to be formed at the same rate and thus prevent the osmotic values from falling.

Returning again to a consideration of the influence of soil moisture content upon the osmotic value of the cell sap it may be pointed out that Iljin, Nazarova, and Ostrovskaja (1915, 1916) and others have reported a close correlation between increases in the osmotic pressure of plant cells and diminution in the water-supplying power of the environment. Hawkins, Matlock, and Hobart (1933) observed that the osmotic pressure and specific conductivity of the leaf sap of the *Acala* variety of cotton were usually inversely correlated with the available moisture supply. At certain times, however, they found that other factors modifying the transpiration rate affected these plant properties more than did the soil moisture conditions.

In general, the higher the moisture content of the soil the lower the osmotic pressure of the roots. The osmotic pressure of the leaves was frequently found to be higher than that of the roots and not always correlated with the latter although it too was markedly influenced by conditions of humidity. McCool and Millar (1917) observed that the moisture content of soils is closely correlated with the depressions of the freezing point of sap from corn, peas, and clover roots. The tops, however, were far less sensitive to variations in the soil moisture content. It is probable that if it were possible to make periodic determinations of the osmotic values of the cell sap of the roots of *Larrea*, as was done with the leaves, an even closer correlation would be found between the variations in soil moisture and the concentrations of the sap. Since all of the environmental conditions, except moisture content, are much less variable for the roots than for the aerial portions of the plant, it is to be expected that the former will respond more quickly and to a greater degree to variations in the available soil moisture.

That there is no set rate of change in response to changes in the environmental conditions seems evident from the data obtained during this investigation. The factors which determine the rate of change do not reside primarily inside the plant but are external to it. Differences such as existed between any of the areas studied were not of sufficient magnitude to produce perma-



nent changes within the plants which would alter their response to variations in the environmental conditions as measured by determinations of their osmotic values from time to time. Any difference in rate of change in cell sap concentration as between plants on different areas could always be attributed to some condition, usually soil moisture content, external to the plant. It would be very difficult to find two creosote bushes which would not respond similarly to all influences of the environment if it were possible to transplant them into identical situations. In other words, there is nothing in this study to indicate that *Larrea* grows in habitats which are sufficiently different to require or produce fundamental and permanent variations in its internal adjustments—, variations, for example, which would cause the plant to respond more rapidly or less rapidly than a sister plant to a given range of environmental factors.

That it is possible temporarily to produce such plants experimentally is well known. Magistad and Truog (1925) were able to lower the freezing point of sap from corn plants as much as two degrees centigrade by applying fertilizer to the hill. This amount of change in the sap concentration was found sufficient to protect young corn seedlings in most cases from late spring frosts. The addition of mineral nutrients to soils, McCool and Weldon (1928) found, generally resulted in increased concentration of the same elements in the cell sap and consequently an increase in the osmotic value of the cell sap. Plants which have undergone a hardening process by exposure to gradually increasing lower temperatures are able to withstand sudden extreme drops in temperature much more successfully than plants which have not become "hardened." These changes, however, are quite temporary.

The rapidity with which all of the creosote bushes studied approach approximately the same osmotic values, as extreme conditions are approached, indicates that all plants of *Larrea* possess a fairly definite range of osmotic value variation. It is possible that had conditions of drought been more severe greater difference in the range of osmotic values for the respective areas would have been found. It is doubtful, however, whether the moisture content of the soil ever gets appreciably lower than it did in the habitats under consideration during the period of this investigation. It is possible, as has already been pointed out, that determinations of the concentration of the root sap might have proven to be a much better measure of the effectiveness of environmental differences on the various areas. Meyer (1929) has shown that unless the differences between two or more habitats is very great, the osmotic value of the expressed sap is not a dependable indicator of the type of environment.

In speaking of the investigation of the peculiarities of habits and physiological activities, Spalding (1904) wrote, "It is certain that a fairly intimate knowledge of even a limited number of desert species brings the conviction

that no general statement is an adequate expression of the biological relations of any one of them, that each is a law to itself, and that its actual relations to the environment must be determined for each species by critical study of its own structural and physiological characteristics, one by one."

The writer hopes that the results of this investigation will prove to be at least stepping stones toward a more complete knowledge of the relations of the creosote bush, *Larrea tridentata*, to its environment.

#### SUMMARY AND CONCLUSIONS

The purpose of the work reported in this paper was to determine the range and differences in the rate of change of osmotic values occurring in *Larrea tridentata*, a non-succulent, perennial, desert shrub, under natural conditions of growth, and to attempt to correlate these variations in range and rate of change with conditions of the environment. Although considerably more experimental work is necessary fully to accomplish this purpose, the following conclusions may be drawn from the data presented:

1. The maximum responses to the extreme changes in the environment are reflected in the osmotic values of the leaves of all creosote bushes in approximately the same length of time regardless of differences in the environmental conditions affecting the bushes during the period between the extremes. The rate of change in osmotic value is regulated by external and not by internal factors.
2. At the end of the rainy season the osmotic values of the leaf sap of creosote bushes in the region studied approach the minimum values and are practically equal in the different areas although rather wide differences may occur at intervals previous to this time. The same relationship holds with respect to the maximum osmotic values at the close of the arid seasons.
3. There are greater differences in the osmotic values of different creosote bushes during periods of drought when the maximum values are approached than during rainy seasons when changes in the osmotic pressures are in the direction of the minimum values. This may be attributed to the possibility that the reactions of a plant are more greatly influenced by individual differences as the dessication of the tissues progresses.
4. Specimens of *Larrea tridentata* from different habitats display ranges of osmotic values for the leaf saps which are relatively specific for each habitat.
5. The greater the range of osmotic value for a given creosote plant or habitat the more successful and uniform the growth of *Larrea*.
6. Conditions of the environment other than rainfall or soil moisture content exert a strong influence on the osmotic value of the cell sap of leaves of *Larrea*, especially as the lowest and highest values are approached.
7. Layers of caliche near the surface are beneficial to those creosote

bushes the roots of which are able to penetrate the caliche, thus drawing upon the moisture stored beneath this layer.

8. *Larrea* bushes in different habitats exhibit approximately the same "osmotic inertia."

9. Variations in the total soluble salt content of the soil at 15 centimeters show from time to time, no correlation with the variations in the osmotic values of the leaves and small twigs of *Larrea* collected on the same dates.

10. The higher the total soluble salt content at 15 centimeters, within the limits of concentration found for the areas studied, the more successful the growth of the creosote bush.

11. The presence of "caliche" in close proximity to the root system does not effect the absorption of calcium by *Larrea tridentata*.

12. There is no correlation between the percentages of CaO and MgO contained in creosote plants, or the Ca/Mg ratios, and the range of osmotic values, or changes in the osmotic values, of the sap of leaves and small twigs of *Larrea*.

13. Collections of plant material for comparative sap concentration studies should all be made at as nearly the same time of day as possible because of the relatively large variations which occur throughout each 24-hour period.

14. During extreme conditions, differences in osmotic values of as much as 8 atmospheres may exist in the sap of different *Larrea* bushes in the same habitat.

#### LITERATURE CITED

- Association of Official Agricultural Chemists.** 1925. Official and tentative methods of analysis. Compiled by the committee on editing methods of analysis. Revised to July 1, 1924. Ed. 2, 535 p., illus. Washington, D. C.
- Bouyoucos, G. J.** 1928. Making a mechanical analysis of soils in 15 minutes. *Soil Sci.* **25**: 473-480.
- Breazeale, J. F.** 1930. Maintenance of moisture-equilibrium and nutrition of plants at and below the wilting percentage. Univ. of Arizona Coll. of Agri., Agr. Exp. Sta., Tech. Bul. 29.
- **and H. V. Smith.** 1930. Caliche in Arizona. University of Arizona, College of Agriculture, Agricultural Experiment Sta. Bul. 131, pp. 419-441.
- Briggs, L. J. and J. W. McLane.** 1907. The moisture equivalent of soils. U. S. D. A. Bur. of Soils, Bul. 45.
- **and H. L. Shantz.** 1912. The wilting coefficient of different plants and its indirect determination. U. S. D. A. Bur. of Pl. Ind., Bul. 230.
- Cannon, W. A.** 1911. The root habits of desert plants. Carnegie Inst. Wash. Publ. 131.
- Chandler, W. H.** 1913. The killing of plant tissue by low temperature. Mo. Agr. Exp. Sta. Res. Bul. 8, pp. 141-309.
- Davis, R. O. E.** 1927. The use of the electrolytic bridge for determining soluble salts. U. S. D. A. Dept. Cir. 423, pp. 1-13. Illus.
- Dixon, H. H.** 1910. Transpiration and the ascent of sap. *Prog. Rei. Bot.* **3**: 1-66.

- Gail, F. W. 1926. Osmotic pressure of cell sap and its possible relation to winter killing and leaf fall. *Bot. Gaz.* **81**: 434-445.
- Harris, J. A. 1915. An extension to  $5.99^{\circ}$  of tables to determine the osmotic pressure of expressed vegetable saps from the depression of the freezing point. *Am. Jour. Bot.* **2**: 418-419.
- and R. A. Gortner. 1914. Notes on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of P for  $\Delta = 0.001^{\circ}$  to  $\Delta = 2.999^{\circ}$ . *Am. Jour. Bot.* **1**: 75-78.
- , J. V. Lawrence, and R. A. Gortner. 1916. The cryoscopic constants of expressed vegetable saps as related to local environmental conditions in the Arizona deserts. *Physio. Res.* **2**: 1-49.
- Hawkins, R. S., R. L. Matlock and C. Hobart. 1933. Physiological factors affecting the fruiting of cotton with special reference to boll shedding. *U. of Ariz. Agr. Exp. Sta. Tech. Bul.* 46.
- Herrick, E. M. 1933. Seasonal and diurnal variations in the osmotic values and suction tension values in the aerial portions of *Ambrosia trifida*. *Am. Jour. Bot.* **20**: 18-34.
- Hibbard, R. P., and O. E. Harrington. 1916. Depression of the freezing point in triturated plant tissues and the magnitude of this depression as related to soil moisture. *Physio. Res.* **1**: 441-454.
- Iljin, V. S., P. S. Nazarova, and M. K. Ostrovskaja. 1915. Osmotic pressure in roots and leaves of plants with respect to the moisture contents of their habitats. *Bul. Acad. Imp. Sci. Petrograd*, 6 ser., **9**: 749-768; abst. in *Exp. Sta. Rec.*, **35**: 733. 1917.
1916. Osmotic pressure in roots and in leaves in relation to habitat moisture. *Jour. Ecol.* **4**: 160-173.
- Korstian, C. F. 1924. Density of leaf sap in relation to environmental conditions in the Wasatch Mountains of Utah. *Jour. Agr. Res.* **28**: 845-909.
- Lewis, G. N. 1908. The osmotic pressure of concentrated solutions and the laws of the perfect solution. *Jour. Amer. Chem. Soc.* **30**: 668.
- Lyon, T. L., and H. O. Buckman. 1922. The nature and properties of soils. Macmillan.
- Magistad, O. C., and J. F. Breazeale. 1929. Plant and soil relations at and below the wilting percentage. *Univ. of Ariz. Coll. of Agri. Agri. Exp. Sta., Tech. Bul.* 25.
- and E. Truog. 1925. The influence of fertilizers in protecting corn against freezing. *Jour. Am. Soc. Agron.* **17**: 517-526.
- McCool, M. M., and C. E. Millar. 1917. The water content of the soil and the composition and concentration of the soil solution as indicated by the freezing point lowerings of the roots and tops of plants. *Soil Sci.* **3**: 113-138.
- and M. D. Weldon. 1928. The effect of soil type and fertilization on the composition of the expressed sap of plants. *Jour. Amer. Soc. Agron.* **20**: 778-793.
- McGeorge, W. T. 1929. The influence of manganiferous soils on the accuracy of the quinhydrone electrode. *Soil Science* **27**: 83-88.
- Meyer, B. S. 1927. Studies on the physical properties of leaves and leaf saps. *Ohio Jour. Sci.* **27**: 263-288.
1929. Some critical comments on the methods employed in the expression of leaf saps. *Plant Physio.* **4**: 103-111.
- Scott, Wilfred W. 1917. Standard methods of chemical analysis. 2nd ed., revised. D. Van Nostrand Company, New York.
- Shantz, H. L., and R. L. Piemeisel. 1924. Indicator significance of the natural vegetation of the southwestern desert region. *Jour. Agr. Res.* **28**: 721-802. 14 pl.



- Spalding, V. M.** 1904. Biological relations of certain desert shrubs. I. The creosote bush (*Covillea tridentata*) in its relation to water supply. *Bot. Gaz.* **38**: 122-138.
1909. Distribution and movements of desert plants. *Carnegie Inst. Wash. Pub.* 113.
- Ursprung, A., and G. Blum.** 1916. Über die Verteilung des Osmotischen Wertes in der Pflanze. *Ber. der Deutsch. Bot. Ges.* **34**: 88-104.
- Walter, H.** 1929. Neue Gesichtspunkte zur Beurteilung der Wasserökologie der Pflanzen. *Ber. der Deutsch. Bot. Ges.* **47**: 243-252.
1931. Die kryoskopische Bestimmung des osmotischen Wertes bei Pflanzen. *Handbuch der biologischen Arbeitsmethoden. Abt. XI. Teil 4, S.* 353-371.
- Whitfield, C. J.** 1932. Osmotic concentrations of chaparral, coastal sagebrush, and dune species of Southern California. *Ecology* **13**: 279-285.



THE EFFECTS OF BLACK LOCUST ON ASSOCIATED  
SPECIES WITH SPECIAL REFERENCE  
TO FOREST TREES<sup>1</sup>

By A. G. CHAPMAN

Central States Forest Experiment Station,  
Columbus, Ohio.

<sup>1</sup> Contribution from Department of Botany, the Ohio State University, in collaboration with the Central State Forest Experiment Station, No. 341. Dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of the Ohio State University.

## CONTENTS

	PAGE
INTRODUCTION .....	39
PLANTATIONS .....	41
Methods .....	41
Results and Discussion .....	42
GARDEN PLOTS .....	52
Methods .....	52
Results and Discussion .....	53
SUMMARY .....	58
LITERATURE CITED .....	59



## THE EFFECTS OF BLACK LOCUST ON ASSOCIATED SPECIES WITH SPECIAL REFERENCE TO FOREST TREES

### INTRODUCTION

For a number of centuries, it has been known among agriculturists that such crop plants as beans, peas, and clover lead to increased yields of certain other crop plants following in the rotation; but it remained for modern investigators to demonstrate that nodule formation on roots of leguminous species is due to infection by nitrogen-fixing bacteria and that through the activity of these bacteria the nitrogen content of the soil is increased. Beijerinck (1888) isolated and cultured the organism and named it *Bacillus radicola*; Prazmowski (1889) changed the name to *Bacterium radicola*; and later the Society of American Bacteriologists placed *Bacterium radicola* in the genus, *Rhizobium*, that commonly in use at present.<sup>2</sup> Fred, Baldwin, and McCoy (1932) have assigned all leguminous species, whose nodule bacteria have been studied, to sixteen groups on the basis of interinoculations; thus, each species within a group may successfully be inoculated with bacteria from the nodules of any other species within the category. The bacteria inoculating roots of species in any one group are deemed distinct enough from those inoculating other groups to be considered as a separate species. Black locust (*Robinia pseudoacacia* L.) alone comprises "Group XII."

The exact process involved in nitrogen fixation by nodule bacteria is not yet understood. Maze (1898) believed that the slimy sheath of the organism, a product of sugar decomposition, combined with the atmospheric nitrogen resulting in the nitrogenous compound absorbed by plants. Spratt (1919) states, "The production of slime is connected with the amount of nitrogen fixed, and is influenced by the medium in which the bacteria are living." Blom (1931) investigated the three possible chemical processes by which nitrogen may be fixed in the organisms, oxidation, reduction, and direct union of nitrogen with some organic compound, and concluded that the fixation occurs through a reduction process. All of his evidence in support of this theory is indirect. According to Fred, Baldwin, and McCoy, "the process of nitrogen fixation begins as soon as, or shortly after, the formation of the nodules and continues as long as the nodules remain firm and healthy, and the plant is actively growing." Numerous authors investigating nitrogen fixation have concluded that after the fixation processes are completed the nitrogen does not become available to green plants until after the death and decomposition of the nitrogen fixing bacteria.

Although foresters have reported, during the last decade, their recognition of the importance of black locust as a benefactor to associated tree species, their data represent studies on comparatively few plantations with

<sup>2</sup> *Pseudomonas radicola* is another name occasionally used.

associated species, primarily catalpa. Ferguson (1922), from studies of adjacent black locust and catalpa plantings at College Farm, State College, Pennsylvania, showed small but consistent decreases in total nitrogen content of the soil at increasing distances from the locust planting. Averages of three nitrogen determinations on soil samples taken in the black locust planting, in the adjacent tall catalpa, and in the catalpa farthest from the locust were, respectively, 0.102, 0.098, and 0.089 per cent. Ranges of average height and diameter<sup>3</sup> measurements of trees in nine successive rows away from the locust were 26.8 to 5.0 feet and 3.3 to 0.7 inches, respectively.

McIntyre and Jeffries (1932), since the collection of data in the present paper, also, have reported recent studies of soil nitrogen in relation to height and diameter growth on two catalpa plantings adjacent to black locust at the Pennsylvania State College, State College, Pennsylvania. For the first plot, the average height for rows 1, 2, 4, 6, 8, and 9 from the black locust planting ranged from 25.8 to 11.4 feet and the average diameter from 4.20 to 1.91 inches; and for rows 1, 2, 4, 6, and 8 of the second plot from 25.1 to 14.0 feet and 3.46 to 2.53 inches, respectively. Both total and nitrate nitrogen analyses were made on soil samples from each plot. The percents of total nitrogen in the first plot found from samples taken in the locust grove, between the first and third rows of catalpa from the locust grove, and between the seventh and ninth rows of catalpa were 0.1463, 0.1316, and 0.1263. The amounts of nitrate nitrogen in the same samples were, respectively, 8.2, 8.9, and 1.8 parts per million of air dry soil before incubation, and 75.3, 68.7, and 36.9 after incubation for thirty days at 22 to 25° C. with a moisture content of the growth media of about 22 per cent. Their check data from an adjacent oak woodlot have not been included. Results of studies on the second planting were quite as indicative of the effects of locust on height and diameter growth of catalpa and nitrogen content of soil as those of the first planting.

Black locust may become established under varying combinations of site factors. Cuno (1930) suggests that the range of black locust may have been originally restricted to the Appalachian Mountains from Pennsylvania to Georgia and to parts of western central Arkansas and eastern central Oklahoma. He further states that the best development of the species occurs on the western slopes of the Appalachians in West Virginia. This tree has been introduced into practically every state for one or another of its many uses. In the western states, eminent success with plantations has been attained in the valleys of the northern Rocky Mountain region, particularly, in Idaho, eastern Oregon and Washington. Black locust was introduced into Europe in 1601 and has been considered the most successful of tree species introduced from America. Although establishment of locust is often found on badly eroded, rocky slopes, the high rates of growth usually occur only in planted or natural stands on well drained silty loams.

The writer found from observations throughout the states of Ohio and

<sup>3</sup> Tree diameters are measured at a height of four and one-half feet from the ground.

Indiana, during the summers of 1931 and 1932, that the black locust-catalpa combination is the usual one from which comparative measurements may be obtained. Suitable plantations were also found, however, when data on the relation of locust to the growth of white ash, tulip poplar, black and chestnut oaks were collected.

The purpose of the present investigation was to obtain more critical data to demonstrate to what extent black locust affects the soil nitrogen content and the growth rate of associated species. Studies have been confined to plantings of species adjacent to locust in the states of Ohio and Indiana and recently established plots in the Botanic Garden at The Ohio State University.

The writer wishes to express appreciation to Dr. E. N. Transeau and Dr. H. C. Sampson of the Department of Botany, The Ohio State University, and to members of the Central States Forest Experiment Station staff, collaborating in the study, for helpful suggestions and criticism during the progress of the investigation.

#### PLANTATIONS

Six plantings have been included in the major part of this investigation; one in Highland County, Ohio; one in Clermont County, Ohio; and four in Clark County, Indiana. Several other plantings in various counties of Ohio have been supplemented for less detailed study. All of these have been established twenty years or more.

*Methods.* Rectangular plots were laid out in representative parts of the plantations adjoining the black locust. In every case, the trees were spaced at regular intervals in rows paralleling those of the locust, and the widths of the plots were sufficient to include from 6 to 20 trees in each row. By using a Forest Service hypsometer and a diameter tape, the height and diameter of each tree on the plots were obtained. Later, the mean height and diameter were calculated for each row.

In the collection of the soil samples at regular intervals of distance from the locust, care was exercised to remove the litter and duff to the mineral soil. Each sample, a composite of four to six samples well distributed across the plot, was taken from the upper 6 inches of the profile, placed in cardboard containers, and immediately treated with a few drops of toluol to stop bacterial action. Within a few hours all samples were thoroughly air dried by spreading out on sheets of paper. Previous to the analytical work, the soil was pulverized and sieved through a 10-mesh screen.

Total nitrogen determinations were made in duplicate on 10-gram soil samples from each collection by the boric acid modification of the Kjeldahl method.

Hydrogen-ion concentrations for the several soil samples were obtained by means of a quinhydrone potentiometer. Ten-gram quantities were each well agitated in 100 cc. of distilled water, the bottles stoppered, and allowed

to stand for twenty-four hours before making the determinations (Ref. in Bailey).

Increment borings<sup>4</sup> were taken from trees near to and at a distance from the locust in six Ohio catalpa plantings. From the cores, a comparison was made of the growth rate for the first 10-year and the last 10-year periods of the two groups.

During the summer of 1931, observations were made on relative degrees of nodulation on grazed and ungrazed locust plantings and also in plantings on various soil types.

*Results and Discussion.* The greater portion of the results from the study of the plantations are presented in eight figures and three tables. Figure 1

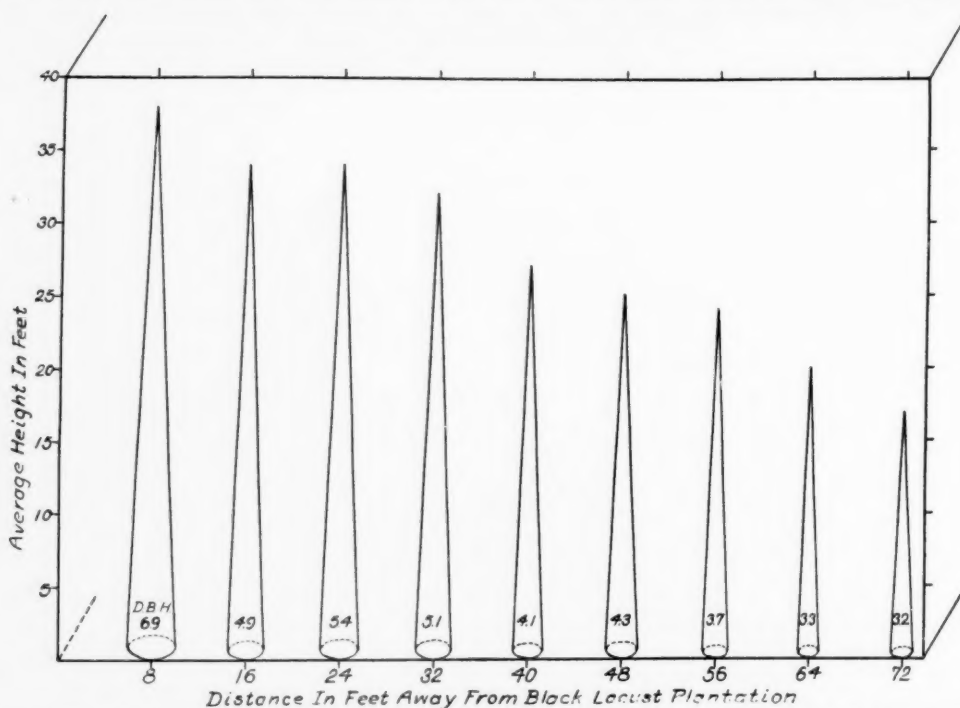


FIG. 1. Average heights and diameters for twelve catalpa trees in each of nine rows at increasing distance from black locust in plot 3.

contains average height and diameter data collected on plot 1 in the catalpa (*Catalpa speciosa*, Warder) planting situated between two black locust plantings in Clermont County. Figure 2 clearly shows the V-shaped dip in the canopy of the catalpa, the shortest stems growing midway between the locust plantings. The arrow designates the first row of black locust on the right; the first row on the left is just beyond the limit of the figure. Annual ring counts showed each species to be 21 years old. The area is generally level with slight surface drainage to the east. As no grazing has occurred since

<sup>4</sup> Increment borings, showing annual rings from the pith to the cortex, were taken at 8 inches from the ground.





FIG. 2. Cross-section of catalpa planting, containing plot 3, situated between two black locust plantings; arrow designating first row of locust on right; locust on left just outside margin of figure.

TABLE 1. Average heights and diameters for trees in rows at increasing distance from black locust in plots 2, 3, 4, 5, 6, and 7.

Plot-2 (Catalpa)			Plot-3 (Catalpa)			Plot-4 (White Ash)			Plot-5 Tulip poplar Black oak			Plot-6 (White ash)			Plot-7 Tulip poplar Black oak Chestnut oak		
Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.
Feet	Feet	Ins.	Feet	Feet	Ins.	Feet	Feet	Ins.	Feet	Feet	Ins.	Feet	Feet	Ins.	Feet	Feet	Ins.
6	40	6.0	6	44	7.5	5	49.0	6.4	5	52.5	7.5	5	52.5	4.7	5	53.5	5.2
12	40	5.8	12	45	7.8	10	41.0	4.1	10	x	x	10	49.7	4.0	10	x	x
18	39	5.2	18	43	7.5	15	39.0	2.9	15	59.7	8.3	15	62.0	5.4	15	46.2	5.3
24	37	5.5	24	42	7.6	20	45.0	4.6	20	x	x	20	x	x	20	x	x
30	35	4.9	30	36	5.4	25	x	x	25	x	x	25	38.5	3.1	25	52.0	6.4
36	35	4.9	36	35	5.5	30	32.5	3.2	30	46.5	5.9	30	45.0	4.2	30	41.0	3.8
42	33	4.9	42	35	5.5	35	44.0	4.7	35	51.0	7.3	35	34.0	3.4	35	40.5	3.8
48	32	4.8	48	31	4.8	40	43.5	4.7	40	43.0	5.3	40	x	x	40	39.0	3.5
54	33	4.6	54	27	4.9	45	41.5	4.7	45	32.0	3.2	45	33.5	2.8	45	24.5	2.5
60	33	5.0	60	31	5.5	50	31.0	3.5	50	43.0	4.8	50	34.7	3.3	50	40.0	3.7
66	31	4.3	66	.....	.....	55	24.0	2.3	55	35.5	3.8	55	30.3	2.9	55	34.5	3.7
72	31	4.6	72	.....	.....	60	18.7	1.6	60	29.0	2.6	60	32.5	3.2	60	x	x
78	31	4.7	78	.....	.....	65	23.0	2.2	65	27.5	2.7	65	27.5	2.6	65	x	x
84	31	4.4	84	.....	.....	70	25.2	2.6	70	34.5	3.9	70	35.5	3.8	70	25.3	3.1
						75	29.6	3.3	75	32.0	2.5	75	27.0	2.7	75	x	x
						80	24.1	2.6	80	x	x	80	26.7	3.0	80	21.5	1.4
						85	25.5	3.0	85	34.0	3.0	85	24.0	2.5	85	25.0	2.7
						90	19.2	2.3	90	35.0	3.2	90	21.5	2.1	90	26.7	3.4
						95	26.5	2.8	95	34.7	3.1	95	25.0	2.8	95	26.0	3.0
						100	19.8	2.2	100	32.0	3.2	100	24.0	2.5	100	24.0	3.3
						105	19.6	2.6	105	33.8	3.2	105	20.0	2.1	105	23.0	2.5

the plantings were made, the Clermont silt loam is well aerated in the upper horizons. Decomposing litter has resulted in accumulation of humus from one-eighth to one-fourth inch in thickness. The greater portion of this humus formed beneath the locust.

Table 1 shows the mean heights and diameters for successive rows of catalpa in Highland County plots 2 and 3, established, respectively, on the west and east sides of the intervening black locust plantation. Figure 3 includes a part of plot 3 which shows the taller locust grove at the left and the catalpa on the right; the arrow marks the first row of catalpa. A very notice-



FIG. 3. Cross-section of plot 2, locust planting on left and catalpa on right; arrow pointing to first row of catalpa.

able decrease in the height of the catalpa is evident with increasing distance from the locust. From increment borings, the age of each species was found to be 25 years. The stand is growing on Clermont silty clay loam which has been slightly compacted by occasional grazing. A very gentle slope drains the area to the northeast.

Table 1 also contains mean height and diameter measurements on the Clark County plots 4, 5, 6, and 7. Plots 4 and 6 were located in pure stands of white ash (*Fraxinus americana* L.), plot 5 in mixed stand of tulip poplar (*Liriodendron tulipifera* L.) and black oak (*Quercus velutina* Lam.), and plot 7 in a mixed stand of tulip poplar, black oak, and chestnut oak (*Quercus montana* Willd.) These stands are 25 year old plantings situated on either side of two locust plantings of the same age. A gentle slope drains the area to the southeast. The soil, Rossmoyne silt loam, is well aerated in the upper part of the profile.

Although there are numerous minor irregularities in the trend of mean tree heights and diameters (Table 1, plots 4 to 7), Figures 1, 2, and 3 and Table 1 distinctly indicate for each plot a decrease in the dimensions of all species as the distance from the locust plantings increases. Recognizing that situations upon which investigations of this nature may be made are infrequent, the writer was careful to select for study those in which differences in topography, soil type, degree of pasturing, and age of locust and adjacent species played no significant rôle. It may be noted that for the Clark County plots data are lacking for a few of the rows. In these instances, there were too many overtopped trees to obtain representative average heights and diameters.

Figure 4 gives the results of total nitrogen analyses on the series of soil

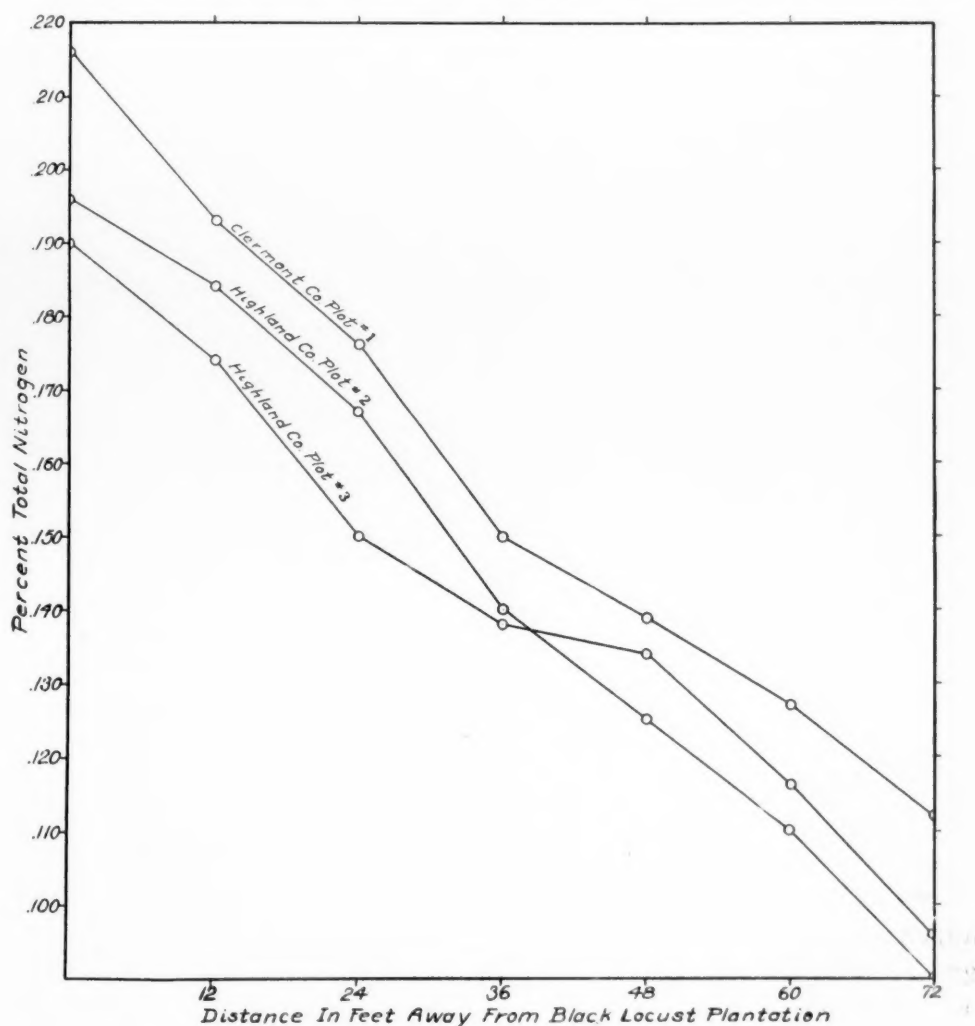


FIG. 4. Percentage of total nitrogen based on 10-gram air dry soil samples from plots 1, 2, and 3.

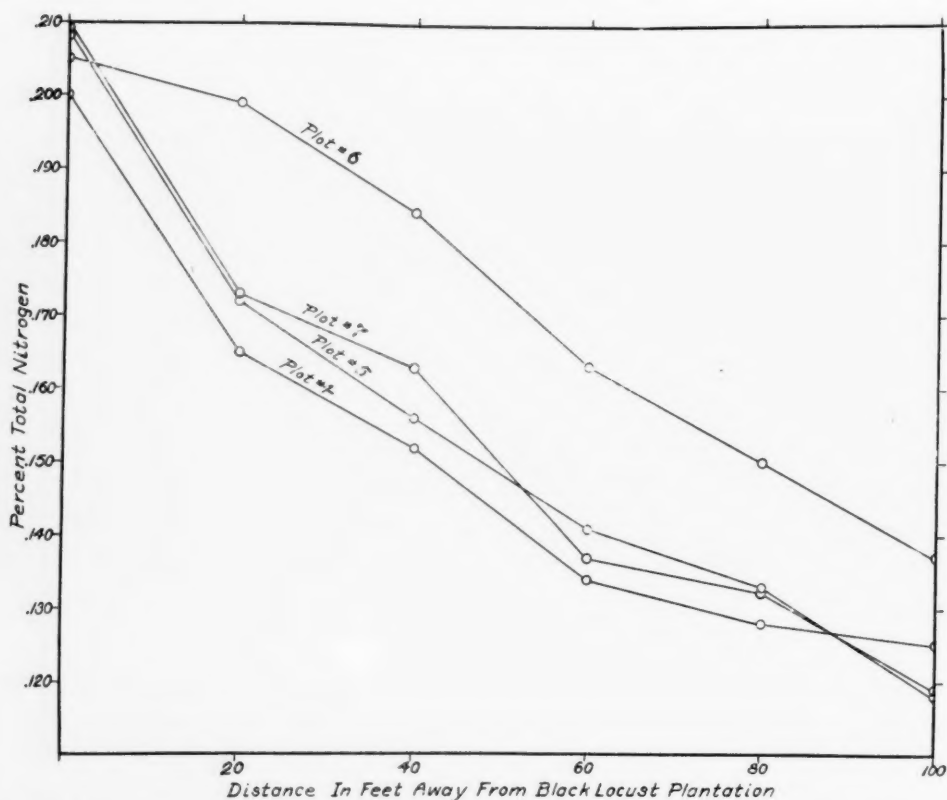


FIG. 5. Percentage of total nitrogen based on 10-gram air dry soil samples from plots 4, 5, 6, and 7.

samples from plots 1, 2, and 3. Figure 5 shows similar data for plots 4, 5, 6, and 7. The figures clearly indicate the rapid decrease in the per cent of total nitrogen content of soil, with increasing distance from the locust. The decrease is somewhat more striking in the plots on Clermont silt loam, a soil type generally very low in organic matter. A range from 0.09 per cent to 0.195 per cent total nitrogen may appear to be small; but, quantitatively, it is equivalent to a range from 1800 pounds to 3900 pounds of nitrogen per acre when based upon two million pounds weight of the top 6 acre-inches of soil. These observed variations in the nitrogen content of the soil and the height and diameter variations of the several tree species on the various plots present a significant correlation.

While the response of the subordinate vegetation to the presence of black locust was of minor importance in the study, Figures 6 and 7, showing orchard grass (*Dactylis glomerata* L.) under catalpa in plot 2, and under adjacent locust, illustrate one of many similar contrasts in growth rates of ground cover species observed by the writer. McIntyre and Jeffries, Cope, and others have reported numerous similar observations. The two exposures (Figs. 6 and 7) were obtained from one set-up at the juncture of the catalpa





FIG. 6. Ground cover of orchard grass west from border of locust in catalpa, plot 1.



FIG. 7. Ground cover of orchard grass east from same position as in Figure 6 but under locust.

and black locust plantings by rotating the camera 180 degrees. On inspection of the two figures, the best measure of differences in the quantity of grass is the depth to which the lower portions of the tree trunks are hidden. The grass becomes sparser under the catalpa as distance from the locust increases. The difference in light intensity under the two species, due to the thinner foliage of the locust than that of the catalpa, is not thought to be a limiting factor here for the growth of orchard grass since the grass development was only slightly better beneath large openings in the catalpa canopy than elsewhere beneath the same species.

The distance to which black locust affects the growth of other species has been little mentioned by investigators. Ferguson states, "Growing among the catalpa trees for a distance of forty feet are black locust trees started as seedlings and as root suckers." It is well understood that these distances will vary directly with the age of the trees and are further modified by such factors as soil aeration, soil moisture, and available essential mineral elements. In Figure 8 are indicated the locations of root suckers in plots 4 and 6 to afford some conception of the root spread of locust in the upper soil horizons. The number of suckers consistently decreases to zero at about 83 feet in plot 6. The gradation is not so characteristic of plot 4. No seedlings could be found on either of the plots. As black locust is quite intolerant to low light intensities, seedlings probably have been oppressed to starvation in the early stages of growth. Root suckers have been able to survive on translocated foods from the parent locust.

Other indications of differences in growth rates of trees adjacent to and at a distance from black locust are given in Table 2. These data consist of measurements of radial increase in inches at stump height of catalpa trees in plot 3, plot 2, and in one planting each in Warren and Green counties. The last two plantings are growing, respectively, in Clermont silty clay loam and Miami silt loam. The highest initial growth rate occurred in the trees of plot 9 adjacent to the locust. It is shown by the mean increments for all plots that the radial increase for the first ten years for the trees near the locust is greater than that for the same period for those trees at a distance. This relationship holds also for the last 10-year period for the same trees. It is clear that the difference in average volume increases is much greater than the radial increases denote. If the spread between the averages of the radial increases for trees adjacent to and trees at a distance from the locust, for each plot, for the first 10-year period be compared with the corresponding spread for the last 10-year period, the latter is shown to be greater. These observations indicate that growth curves based on radial measurements in these plots would, in general, be diverging.

The degree of nodulation on the roots of black locust and hence the

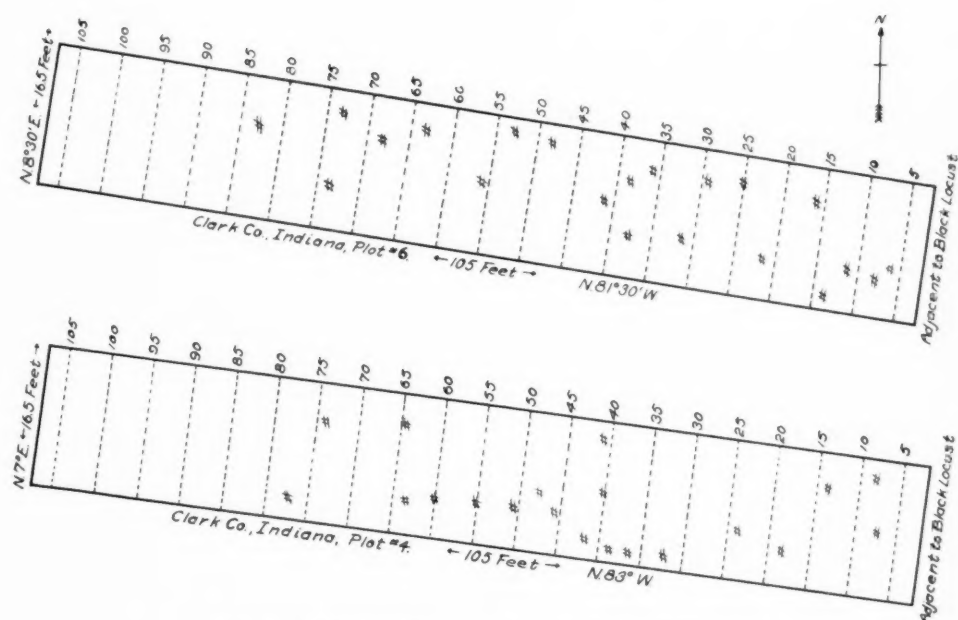


FIG. 8. Distribution of root suckers in plots 4 and 6.

amount of atmospheric nitrogen fixed vary with certain physical conditions in the soil. Examination of many roots in numerous plantings in Ohio and Indiana showed that minimum nodule formation occurred in those areas which were heavily grazed or water-logged for long periods in the year. In the grazed plantings, the few nodules present were small and occurred at the base of trees near the soil surface. Both the old and recently developed tubercles were small. In the water-logged plantings, the few nodules present were mainly in the upper one or two inches of soil, but were distributed much more widely than in the pastured areas. A characteristic common to both the heavily grazed and water-logged soil was poor aeration and, therefore, an insufficient amount of free oxygen for the aerobic nitrogen-fixing bacteria. Clearly, this was the limiting factor in nodulation in these plantings. Nobbe and Hiltner (1899) found that nodules on the roots of black locust, when submerged in water, are of little or no benefit to the host plant.

In the ungrazed plantings, nodulation was at its maximum in well drained, porous, silt loams over which had accumulated layers of humus and leaf litter. The position of most of the nodules in the soil profile was between the mineral soil and the humus or in the upper inch of the mineral soil. In such an environment, the moisture supply was adequate for nodule development even during the dry season of 1931. Where accumulation of humus and litter was scant and periodic drying of the surface soil occurred, the greatest abundance of tubercles was found somewhat deeper; but in no place were many nodules found below a depth of six inches. McIntyre and Jef-

TABLE 2. Radial growth of catalpa at stump height for both first and last ten-year periods, based on six successive trees in rows adjacent to and at different distances from locust.

Plot No.	Near Locust, Growth in Inches		Away from Locust, Growth in Inches		Location and age of plots
	First 10 Years	Last 10 Years	First 10 Years	Last 10 Years	
3	1.80	1.50	72 feet from locust		On Delmar Jester farm, Clermont Co., Ohio. Age 21 years.
	1.40	1.40	1.40	0.75	
	1.95	1.25	1.10	0.70	
	2.05	1.80	1.70	0.60	
	2.00	1.75	1.25	0.65	
	1.60	0.95	1.50	0.65	
	1.60	0.95	1.25	0.55	
Average . . . . .	1.80	1.44	1.36	0.65	
2	1.85	2.15	60 feet from locust		On Edward Raousch Farm, Highland Co., Ohio. Age 24 years.
	2.30	2.10	1.60	1.25	
	2.10	1.75	1.20	0.55	
	2.00	2.00	1.10	0.80	
	2.20	1.60	1.35	0.90	
	2.15	1.60	0.90	0.40	
	2.15	1.60	1.65	0.80	
Average . . . . .	2.10	1.86	1.30	0.78	
8	2.10	1.25	60 feet from locust		On Henry Giehl farm, Warren Co., Ohio. Age 20 years.
	1.70	1.10	1.25	0.70	
	2.05	1.70	1.65	1.10	
	1.70	1.35	1.55	1.20	
	1.50	2.50	1.65	2.10	
	2.00	1.65	1.40	1.35	
	2.00	1.65	1.90	0.95	
Average . . . . .	1.84	1.59	1.56	1.23	
9	3.40	1.40	80 feet from locust		On Theodore and Max Zink farm, Greene Co., Ohio. Age 24 years.
	2.70	1.60	1.75	0.50	
	2.80	1.35	1.95	0.80	
	1.65	1.50	2.40	0.95	
	2.60	1.30	2.05	0.70	
	2.85	1.40	1.85	0.60	
	2.85	1.40	1.85	0.80	
Average . . . . .	2.66	1.42	1.97	0.72	

fries quote Beijerinck (1918) as observing that black locust has few and small nodules. This observation is true for only certain combinations of site factors. The writer has frequently observed nodules in great abundance, a few having dimensions exceeding 0.5 by 0.2 inches.

There is little discrimination to be made on the relative amounts of nodulation by black locust in soil types whose parent materials are of different geological origin, provided such factors as soil moisture, soil aeration, and



organic matter content of soil are approximately equivalent. No definite range of pH tolerance can be cited for the locust bacteria, but it is known to be wider than for the bacteria of some of the field crop legumes. Cope states that the bacteria of black locust are more acid tolerant than those of alfalfa. By growing soy beans under three sets of conditions, "first, by varying the amount of calcium and inversely the degree of acidity; second, by varying only the acidity at constant amounts of calcium; and third, by varying only the calcium at constant acidity," Albrecht (1932) found that increased nodulation accompanied increased available calcium in the "growth media" but did not accompany or follow increased pH. This suggests that a correlation between a pH range and the amount of nodulation for black locust would be of questionable significance. Table 3 represents soil reaction and total nitrogen determinations made on soil samples collected from black locust and adjoining plantations growing on different soil types. It may be noted

TABLE 3. Soil reaction and percentage of total nitrogen of soil samples from locust and adjacent plantings on different soil types in Ohio and Indiana.

Plot location	Soil type	pH		Percentage of total nitrogen	
		Under locust	Under other species	Under locust	Under other species
Clark Co., Indiana					
Plot-4.....	Rossmoyne silt loam.	6.72	7.02	0.200	0.125
Plot-5.....	Rossmoyne silt loam.	6.88	6.45	0.208	0.118
Plot-6.....	Rossmoyne silt loam.	6.79	6.97	0.205	0.137
Plot-7.....	Rossmoyne silt loam.	6.49	6.68	0.209	0.119
Clermont Co., Ohio					
Plot-3.....	Clermont silt loam...	6.46	6.15	0.216	0.112
Highland Co., Ohio					
Plot-2.....	Clermont silty clay loam.....	5.36	5.52	0.192	0.096
Greene Co., Ohio					
Plot-9..... (Catalpa)	Miami silt loam.....	6.44	6.88	0.211	0.182
Morrow Co., Ohio					
Plot-10..... (Catalpa)	Volusia silt loam....	5.33	5.77	0.253	0.194
Morrow Co., Ohio					
Plot-11..... (Catalpa)	Immature soil. Parent material sandstone and shale....	4.44	5.16	0.345	0.139
Delaware Co., Ohio					
Plot-12..... (Catalpa)	Miami silty clay loam.....	5.36	5.28	0.246	0.160

that the pH range in the locust stands is from 4.44 in the immature soil of Morrow County to 6.88 in plot 5. While nodulation was good in all of these plantings, the maximum development of tubercles was beneath a thick humus and in the upper two inches of the immature acid soil in plot 11. There is no indication that the acidity range found in these areas has set any limitations on nodule formation. Hall (1932) found no correlation between soil reaction and degree of nodulation in more than two hundred widely distributed black locust plots.

According to McIntyre and Jeffries, "Black locust does well on the so-called acid soils of Pennsylvania such as DeKalb, Berks, and Volusia, and the authors believe that factors other than soil acidity, particularly the presence of the particular group of bacteria associated with this species, are of more importance." Cope states that special inoculation material is used in New York in many instances to inoculate soil for seeding black locust. During the summer of 1932, the writer examined more than one hundred locust plantings and as many stands of natural reproduction in Ohio, Indiana, and Michigan but failed to find one without enough tubercles present to indicate that inoculation had not occurred. Also, an attempt by the writer to grow locust seedlings in framed plots in the Botanic Garden without root infection by nodule forming bacteria failed, even though the soil had been treated to a depth of one foot with a three per cent solution of formalin one week before seedlings from sterilized soil were planted. Many flats of locust seedlings, growing in the greenhouse in soil media which had been autoclaved at fifteen pounds pressure for four hours, became inoculated with no special attention being given to prevent or effect bacterial transfer. From these experiences, it seems that the bacteria are of such common occurrence that failure of locust to become inoculated is unlikely.

#### GARDEN PLOTS

As preliminary work in the field had clearly demonstrated that black locust is effective in increasing the growth rate of certain associated species, the garden plot study was begun to determine how soon the effects would be perceptible.

*Methods.* Soil, underlain by limestone glacial outwash gravel, was excavated to a depth of 12 inches along a terrace contour for eleven plots 4 feet square and 2 feet apart. Frames constructed from boards 1 inch thick by 14 inches wide were fitted into the excavations so that about 2 inches projected above the ground level. The excavated soil material was returned to the frames by passing through a sieve with one-quarter inch meshes. Care was observed to give all the plots uniform horizontal surfaces.

The seedlings of black locust and Chinese elm (*Ulmus pumila* L.) used for planting were grown from seed<sup>5</sup> in the Department of Botany green-

<sup>5</sup> Seed was obtained from the Katzenstein Seed Company, Atlanta, Georgia.

house. Seeds of locust, dusted with Semesan<sup>\*</sup> for disinfection, had been sown in small flats of sandy soil material which had been sterilized in an autoclave at 15 pounds pressure for 4 hours. The elm seed had been sown in similar flats that had not been sterilized.

The 6 weeks old stock was transplanted to the garden 6 inches apart in rows at the same intervals on June 1, 1931. Only elm was planted in plots 2, 4, 6, 8, and 11 while locust was alternated with the elm in the rows of the remaining six plots. Before setting each locust plant in place, its root system was dipped into an inoculum prepared from fresh tubercles.

In the dry periods of the growing seasons of 1931 and 1932, the plots were occasionally watered and well weeded. As the locust grew more rapidly than the elm, it was necessary frequently to clip those branches exceeding the height of the elm.

Well distributed soil samples were collected from the surface 4 inches in each plot on June 23, July 13, August 9, September 2, September 22, October 12, and November 10 in the second season. These were promptly air dried, sifted through a 10-mesh sieve, and placed in containers for future analysis.

Also, samples of elm leaves were gathered from each plot on the dates of soil collection. Each sample was composed of all ages of leaves from the entire elm population of the individual plots. The last collection was made when the leaves were turning brown and abscising. The samples were dried at 80° C. to constant weight. They were then ground to a powder in a food pulverizer and stored in air-tight cans.

Total nitrogen was determined on 10-gram soil samples and 2-gram leaf samples by the boric acid modification of the Kjeldahl method, previously mentioned.

*Results and Discussion.* Figure 9 shows the fluctuations during the 1932 growing season in total nitrogen content of the soil for each of the pure elm plots. It is evident from inspection of the graphs that in general there was a decrease in the total nitrogen until a minimum was reached about September 2. Although there is an increase in nitrogen content in the plots after the low points, with ensuing decreases of the element in plots 4, 6, and 11, it is evident that on the dates of sampling subsequent to July 13 in no plot does the nitrogen present equal that of June 23. The conditions under which the plants of the various plots developed were deemed sufficiently similar to justify plotting an average of the amounts of nitrogen for each sampling date in order to present more clearly the general trend. These data are shown in the broken line curve.

It may be noted that the lower numbered plots had the higher initial percentages of total nitrogen. From the first plot through the seventh, there was a progressive decrement of organic matter in the soil; whereas for plots 7, 8, 9, 10, and 11 the organic matter was fairly constant.

<sup>\*</sup> Semesan is a proprietary compound with active ingredient of hydroxymecurichlorophenol.

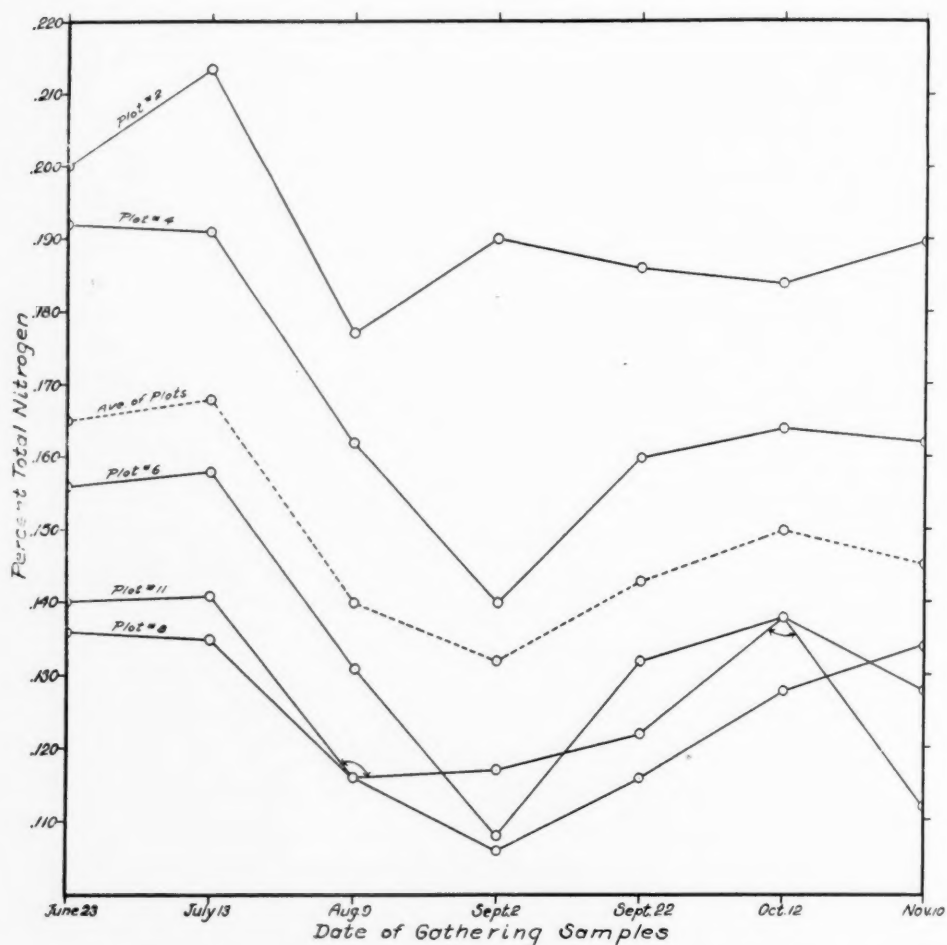


FIG. 9. Fluctuations of percentage of total nitrogen in soil of Botanic Garden elm plots for 1932 growing season.

In accounting for the drop in the total nitrogen content of the soil at the end of the summer, it should be known that the decline coincided with a severe drought for the terrace portion of the garden. As the underlying parent soil material of outwash gravel made underground drainage excessive, watering was not adequate to prevent recurrent soil desiccation to a depth of 3 to 5 inches. Any increases in total nitrogen should be attributed primarily to the non-symbiotic nitrogen-fixing bacteria. Decreases in total nitrogen indicate that absorption of soluble nitrogen compounds by the seedlings has been in excess of fixation of atmospheric nitrogen by the microorganisms.

The fluctuations during the 1932 growing season in total nitrogen content of the soil from the elm-locust plots are shown in Figure 10. The minimum content in general was reached about September 2 for the soil of the plots. During the period from September 2 to September 22, the nitrogen increment for these plots was much greater than for the elm plots. On November

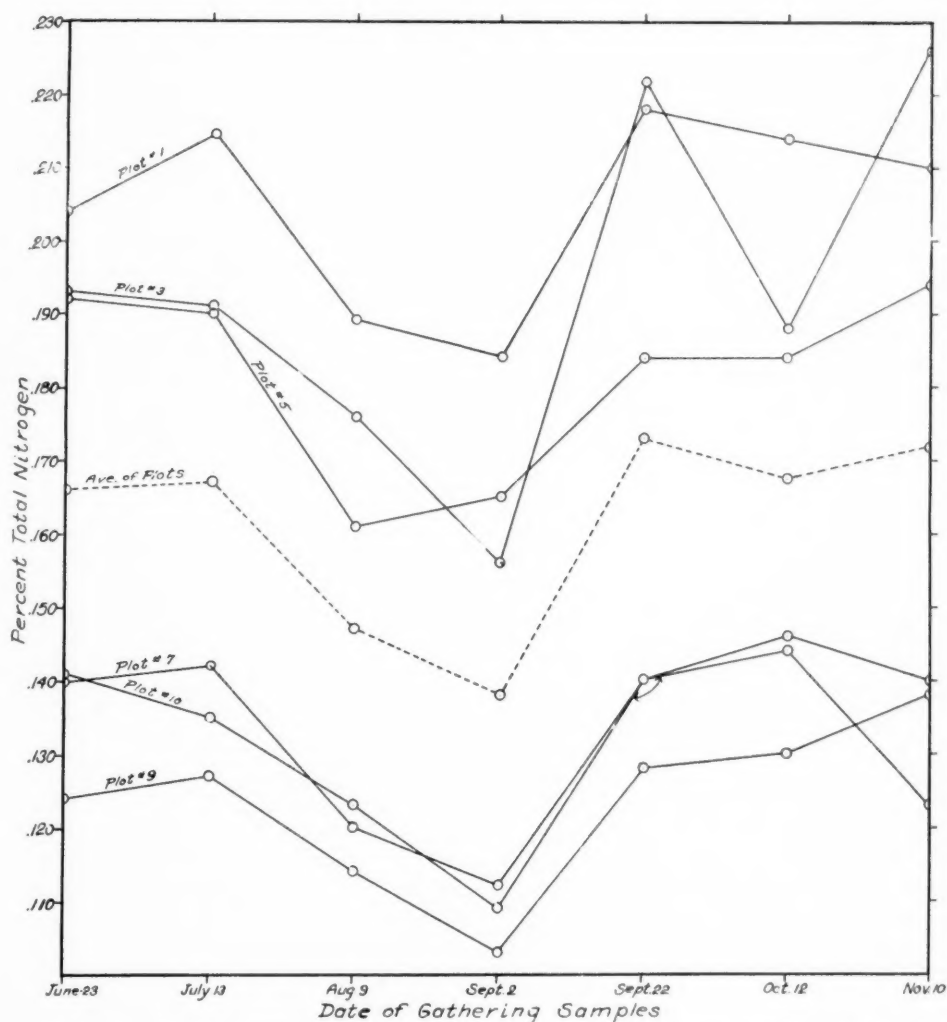


FIG. 10. Fluctuations of percentage of total nitrogen in soil of Botanic Garden elm-locust plots for 1932 growing season.

10, all plots except number 10 were found to have a nitrogen content equivalent to or greater than that on June 23.

As in Figure 9, the broken line curve represents averaged data from all of the plots. The average of analytical results for the initial soil samples is almost identical to the corresponding average of the elm plots, and the total nitrogen reduction on September 2 is less than that for the elm plots on the same date. The final average on November 10 shows a higher total nitrogen content than the corresponding value for the plots with no locust.

Alteration of nitrogen conditions by lateral leaching of soluble organic or inorganic substances or surface drainage into the plots was largely prevented by the sunken frames. The validity of the comparison cannot be discredited by differences in nitrogen absorption by the two species, as the more rapidly developing locust would absorb a greater quantity of nitrogen



than an equal number of less rapidly developing seedlings in the elm plots. In view of these data, it is inferred that the general increase of nitrogen of the elm-locust plots in excess of that of the elm plots is chiefly due to the presence of the black locust seedlings.

Examination of a few of the locust roots a month after transplanting the seedlings to the garden showed many small nodules present. The root systems were restricted to small areas the first year; but, during the second season, extensive fibrous roots with an abundance of large and small nodules developed in the upper 6 inches of soil.

In an effort to further detect any nitrogen changes in the soil material of the two groups of plots ascribable to the presence of locust, a series of

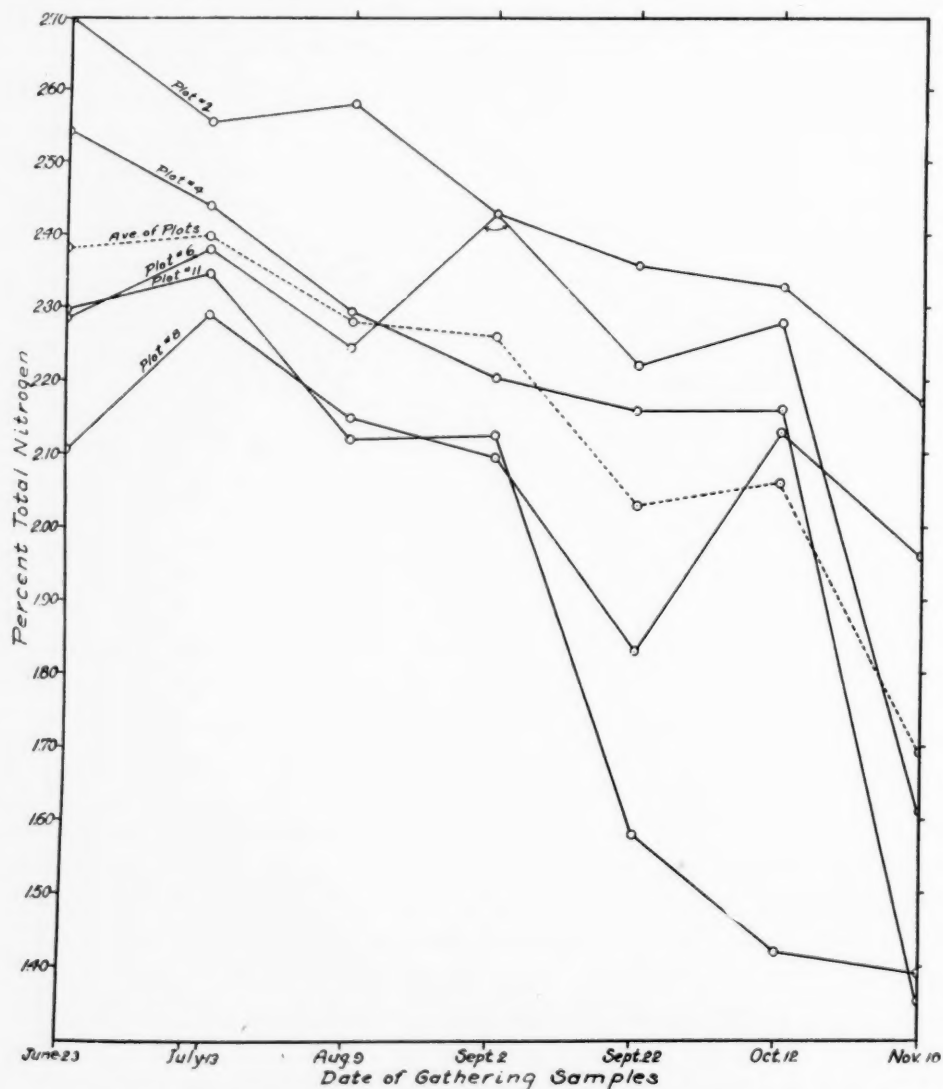


FIG. 11. Fluctuations of percentage of total nitrogen in oven dry elm leaves of Botanic Garden elm plots for 1932 growing season.

nitrogen analyses on the leaves of the associated elm was made. It is generally recognized that seedlings of different tree species behave differently under varying nitrogen conditions of the soil medium. The writer (1931) found that the total nitrogen content of the leaves of elm seedlings (*Ulmus americana* L.), produced under greenhouse conditions, were indicative of the varying quantities of total nitrogen in their soil media. For this reason, an elm species was planted with the locust for the present study.

Figure 11 shows the percentages, based on oven dry weight, of total nitrogen in the leaf samples obtained from the elm plots simultaneous with soil samplings. It is clear from the figure that, aside from the occasional increases in plot 6 and 8, there is a fairly consistent reduction in the leaf nitrogen content throughout the series. The broken line curve, representing average values, verifies this characteristic trend of the individual plot curves.

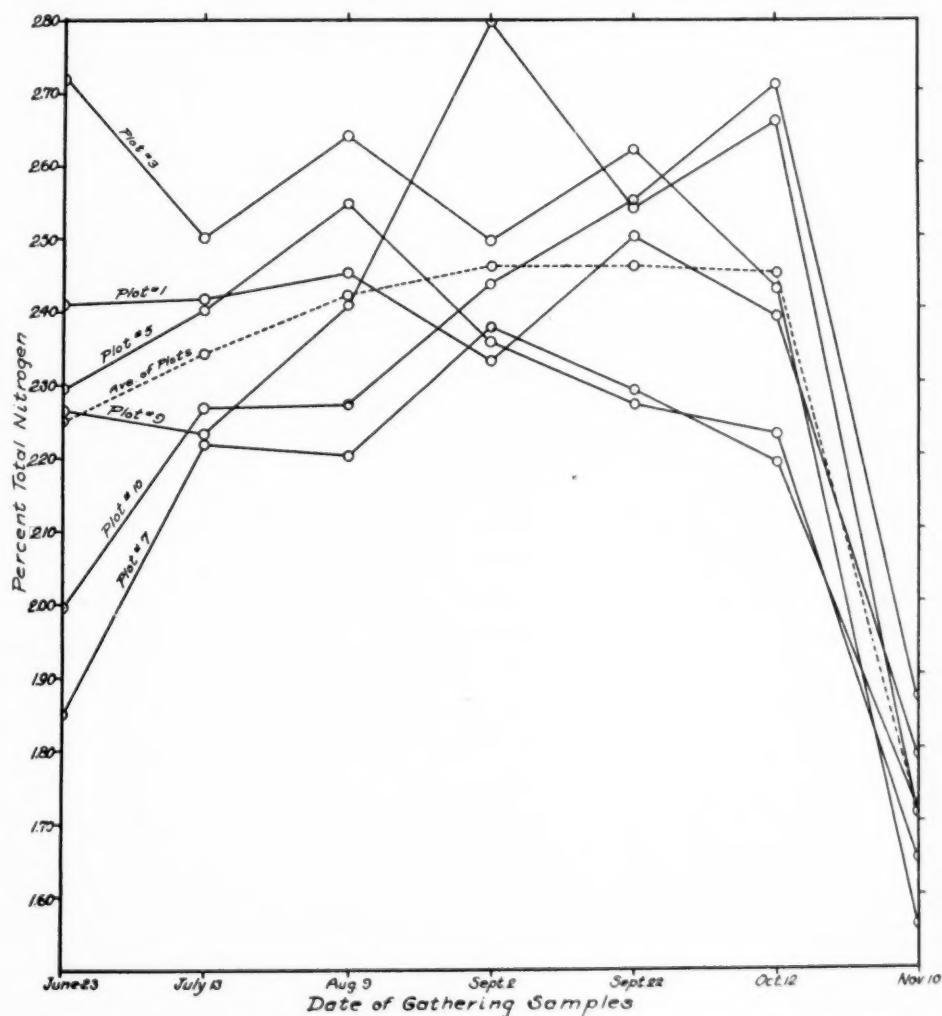


FIG. 12. Fluctuations of percentage of total nitrogen in oven dry elm leaves of Botanic Garden elm-locust plots for 1932 growing season.

Results from nitrogen determination, corresponding in time to the above results but for the elm-locust plots, are shown in Figure 12. For the initial leaf samples, the nitrogen content is generally lower on the elm-locust plots than on the elm plots. This may be partially due to the greater exhaustion, during the spring, of available nitrogen in the soil by the more rapidly growing locust seedling. Since the overshadowing of elm was prevented by clipping off the upper locust branches, it is improbable that the differences in light intensities in the canopies of the pure and mixed plantings was sufficient to produce a difference in the carbohydrate-nitrogen ratios in the elm leaves of the two plantings.

The average plot curve shows; first, a gradual percentage increase of leaf nitrogen until September 2, in contrast to that of the elm plots; second, a constant nitrogen content until October 12; and, third, a sudden drop in total nitrogen on November 10.

The sharp decrease in leaf nitrogen content for nearly all of the plots (Figures 11 and 12) on November 10 is noteworthy. The percentages of nitrogen represented in the two figures for November 10 are based on yellow, abscising leaves. Already existing soluble nitrogen compounds in the leaves, and the soluble forms resulting from processes of decomposition during the yellowing and hence the browning period, apparently move into the stems. However, some of the nitrogen loss to the leaves may be due to leaching by rain. Combes (1926) and others have found increases of nitrogen in stems following the yellowing period in autumn. Ebermayer (1888) and others have found the percentage of nitrogen in fallen leaves less than that in dried green leaves. This decrease of nitrogen content of leaves at the time of abscission then is a common phenomenon and is not peculiar to the conditions of this study.

#### SUMMARY

1. An investigation has been made of the effects of black locust on soil nitrogen and on the growth rates of associated species in forest plantings in Ohio and Indiana. Studies of total nitrogen changes were also conducted during the 1932 growing season on the soil and leaves of elm seedlings of eleven garden plots containing elm in pure stand and in mixture with black locust.

2. In plantings of catalpa, white ash, tulip poplar and black oak, mixed tulip poplar, black oak, and chestnut oak adjacent to black locust, where such site factors as differences in topography, soil types, grazing, and age of locust and adjacent species were irrelevant, appreciable decreases in the heights and diameters of trees with increasing distance from the locust were found.

3. Analyses of soil samples, collected at regular intervals from the locust in each of six Ohio and Indiana plantations, indicated reductions in total

nitrogen as distance increased. These reductions in each plot showed definite correlations with reduction in mean heights and diameters for adjacent trees.

4. Definite decreases in the number and in the degree of development of ground cover species were observed as distance from the locust increased.

5. Increment borings have shown that the differences between the radial increases for the first and last 10-year periods for catalpa adjoining black locust was less than that for the same periods for catalpa at distances from the locust; and that the difference between the radial increases for the first 10-year period for adjacent catalpa and catalpa at distances from the locust was decidedly less than the difference between radial increases for the last 10-year period for the same trees.

6. Nodulation was at a maximum in the upper 4 inches of soil where a moderately constant moisture content, a high percentage of organic matter, and good aeration existed.

7. Although poor nodulation was found in many plantings and in naturally reproduced stands of black locust, evidence from field and garden plot studies indicates that, rather than absence of locust bacteria, poor aeration, poor moisture conditions, or both were the primary causes.

8. No correlation between soil reaction and degree of nodulation was evident from studies in locust plantations growing on different soil types.

9. Significant increases in amounts of total nitrogen were detected during the second growing season in the soil and leaves of elm of the elm-locust garden plots.

10. An appreciable decrease in the total nitrogen content of the soil of the elm plots was found at the end of the 1932 growing season.

11. During the summer of 1932, progressive decreases occurred in the total nitrogen content of the leaves of elm from the garden elm plots.

12. The results of this study provide additional data showing the effects of black locust on species associated with it. The details of the processes involved in the production of these effects have been aside from this study and should be the subject of further investigations.

#### LITERATURE CITED

- Albrecht, W. A. 1932. Calcium and hydrogen-ion concentration in the growth and inoculation of soy beans. *Jour. Amer. Soc. Agron.* **24**: 793-806.
- Bailey, E. H. 1932. The effect of air drying on the hydrogen-ion concentration of the soils of the United States and Canada. *U. S. D. A. Tech. Bul.* 291.
- Beijerinck, M. W. 1888. Die Bakterien der Papilionaceenknöllchen. *Bot. Ztg.* **46**: 103.
1918. The significance of the tubercle bacteria of papilionaceae for the host plants. *Proc. Royal Acad. Science Amsterdam* **21**: 183-192.
- Blom, J. 1931. Ein Versuch, die chemischen Vorgänge bei der Assimilation des molekularen Stickstoffs durch Mikroorganismen zu erklären. *Centbl. Bakt., (etc.)* **2** Abt., **84**: 60-85.

- Chapman, A. G.** 1931. Some effects of varying amounts of nitrogen on the growth of white elm seedlings. Unpublished data. The Ohio State University, Columbus.
- Combes, R.** 1926. Emigration des substances azotees des feuilles vers tiges et les racines des arbres au cours du jaunissement autumnal. *Rev. Gen. Bot.* **38**: 430-448; 510-517; 632-645.
- Cope, J. A.** 1929. Concerning black locust in New York. *Jour. Forestry* **27**: 828.
- Cuno, J. B.** 1930. Utilization of black locust. U. S. D. A. Cir. 131.
- Ebermayer, F.** 1882. "Physiolog. Chemie d. Pflanzen" 1, 737, Berlin.
- Ferguson, J. A.** 1922. Influence of locust on the growth of catalpa. *Jour. Forestry* **20**: 318-319.
- Fred, E. B., I. L. Baldwin, and E. McCoy.** 1932. Root nodule bacteria and leguminous plants. *University of Wisconsin Studies* **5**: 343.
- Hall, R. C.** 1932. Studies on the control of the locust borer. Unpublished data. U. S. Bureau Entomology.
- Maze, M.** 1898. Les microbes des nodosites des Legumineuses. *Ann. Inst. Pasteur*, **12**: 1-25, 128-155.
- McIntyre, A. C., and C. D. Jeffries.** 1932. The effect of black locust on soil nitrogen and growth of catalpa. *Jour. Forestry* **30**: 22-28.
- Nobbe, F., und L. Hiltner.** 1899. Über die Wirkung der Leguminosenknöllchen in der Wasserkultur. *Landw. Vers. Sta.*, **52**: 455-465.
- Prazmowski, A.** 1889. Das Wesen und die biologische Bedeutung der Wurzelknöllchen der Erbse. *Bot. Centrbl.* **39**: 356-362.
- Spratt, E.** 1919. A comparative account of the root nodules of the Leguminosae. *Ann. Bot. (London)*, **33**: 189-199.



# THE ORIGINAL FOREST TYPES OF SOUTHERN NEW ENGLAND<sup>1</sup>

By STANLEY W. BROMLEY

"The path led through woods which bore the mark of centuries, over barren hills that had been licked by the Indians' hounds of fire. . . ."

—*The Old Bay Path*, J. G. Holland.

<sup>1</sup> Papers from Department of Botany, the Ohio State University, No. 336.

## CONTENTS

	PAGE
INTRODUCTION .....	63
ACKNOWLEDGMENTS .....	63
HISTORICAL FACTORS: PRE-COLONIAL .....	64
HISTORICAL FACTORS: THE POST-GLACIAL PERIOD .....	67
HISTORICAL FACTORS: COLONIZATION .....	68
THE PRINCIPAL FOREST REGIONS .....	69
1. Oak Region .....	80
2. The White Pine Region .....	72
3. The Northern Forest Region .....	76
CERTAIN PHYSIOGRAPHIC TYPES IN NEW ENGLAND .....	77
1. Flood Plain and Alluvial Woodland Associations .....	77
2. Pine Plains .....	78
3. Chamaecyparis Bogs .....	79
4. Maple Swamps .....	79
EFFECTS OF PASTURING .....	79
EXAMPLES OF OLD-GROWTH FOREST .....	80
1. Oak Region .....	80
2. White Pine Region .....	82
3. The Northern Forest .....	86
AGES OF FOREST TREES IN THIS AREA .....	86
PRESENT DAY TENDENCIES .....	87
LITERATURE CITED .....	88

## THE ORIGINAL FOREST TYPES OF SOUTHERN NEW ENGLAND

### INTRODUCTION

To reconstruct the appearance of southern New England<sup>2</sup> when the forest was the domain of the Indian, wolf, and rattlesnake is indeed an interesting but difficult problem after the nearly complete obliteration of natural features by more than two centuries of cultivation, grazing, and industrialization. It is the common assumption that most of the country was originally wooded—but what were the forest types, what was the character of the forest, and what were the influences to which it was subjected compared with those of the present day? Obviously, any idea of the original conditions may be gained only through a composite study of the ecology of the present day forest and the meager records of the past.

Inasmuch as the original woodlands were destroyed early in the settlement of the country, little light can be shed on the problem of original types by correlating soil or climatic factors with the present associations, composed as they are largely of secondary species or of secondary communities. The historical factors must therefore be given consideration in outlining the original forest types. The present paper deals largely with this phase.

A method of studying the historical factors may be outlined as follows:

#### A. Prehistoric evidence.

1. Fossil trees and plants.
2. Laminated clay records.
3. Fossil pollen (bog records).

#### B. Historic evidence.

1. Early travelers' records.
2. Early surveyors' records.
3. Local histories.
4. Contemporaneous writings.

Due to the paucity of prehistoric evidence in the region under consideration, little can be said at present. The historic evidence which I shall present has been largely gleaned from nos. 1, 3, and 4 under B.

### ACKNOWLEDGMENTS

The writer wishes to express his sincere thanks to Dr. E. N. Transeau, Chairman of the Department of Botany, Ohio State University, who suggested the preparation of this paper and whose suggestions and timely help have been invaluable; to Dr. R. B. Gordon of the Department of Botany, Ohio State University, Dr. G. E. Nichols and Dr. C. G. Deuber of Yale University, and Dr. R. P. Marshall, all of whom have materially aided the writer in one way or another in the prosecution of this study. I am greatly

<sup>2</sup> Massachusetts, Rhode Island, and Connecticut.

indebted also, to Dr. M. L. Fernald of the Gray Herbarium, Harvard University, for his kind assistance in supplying data on the location of *Chamaecyparis* bogs. The reference work was largely done at the New York City Library, the Colonial Library at New Haven, the Yale University Library at New Haven, the Southbridge Public Library, the Ferguson Library at Stamford, Connecticut, the Ohio State University Library, and the private library of Mr. F. A. Bartlett, Stamford, Connecticut.

#### HISTORICAL FACTORS: PRE-COLONIAL

The picture which may be gained from the writings of the early travelers is fragmentary, but at least it gives a basis for surmise as to the character of the forest at the time of settlement by the whites. On one subject, all are in accord and that is the observation that the original forest was, in most places, extremely open and parklike, due to the universal factor of fire, fostered by the original inhabitants to facilitate travel and hunting. We do not know the exact Indian population of southern New England at the advent of the whites, but it was probably about the maximum that could exist under the conditions of the times. Dwight (III, 31) gave an estimate of about 80,000 distributed over an area of thirty to forty thousand square miles. At any rate, there was probably a sufficient population to bring about an annual burning of most of the country sufficiently dry for a conflagration. The burning of the forests and grasslands, it must be remembered, was a universal custom among aboriginal people, not only in the Americas, but in many other regions of the world as well.

To quote from Thomas Morton<sup>3</sup> (1632), "the Salvages are accustomed to set fire of the country in all places where they come; and to burn it, twice a yeare, vixe, at the Spring, and at the fall of the leafe. The reason that moves them to do so, is because it would be otherwise so overgrown with underweedes<sup>4</sup> that it would be all a copice wood, and the people could not be able in any wise to passe through the country out of a beaten path. . . . The burning of the grasse destroyes the underwoods, and so scorceth the elder trees, that it shrinks them, and hinders their growth very much: So that hee that will look to finde large trees, and good tymber, must not depend upon the help of a wooden prospect to find them on the upland ground; but must seeke for them . . . in the lower grounds where the grounds are wett when the country is fired. . . . For when the fire is once kindled, it dilates and spreads itself against as with the winde; burning continually night and day, until a shower of raine falls to quench it. And this custome of firing the country is the means to make it passable, and by that meanes the trees growe here and there as in our parks: and makes the country very beautifull, and commodius."

Dwight, somewhat more than 150 years later,<sup>5</sup> gives an additional purpose

<sup>3</sup> Chapter XVII. Morton's observations were in east central Massachusetts, in what might be termed the Boston region. He lived until his expulsion from the colonies near what is now Wollaston.

<sup>4</sup> Underwoods?

<sup>5</sup> Many of Dwight's travels took place in the latter part of the eighteenth century and the first part of the nineteenth. His descriptions, however, were not published until 1821.

for the Indian's fires. Although the character of the New England woods had greatly changed by his time as a result of clearing, grazing and other factors incidental to white settlement, he had visited western New York state which had been more recently subject to Indian influence. "The object of these conflagrations was to produce fresh and sweet pasture, for the purpose of alluring the deer. . . . Immediately after the fires a species of grass springs up, sometimes called fire grass."<sup>6</sup> "Of this nature were always the oak and yellow pine grounds: which were therefor usually subjected to an annual conflagration. The beech and maple grounds were commonly too wet to be burned." In Letter VIII, p. 103, the same author states that "The aborigines of New England customarily fired the forests that they might pursue their hunting with advantage . . . the grounds which were covered with oak, chestnut, etc., or with pitch pines, were selected for this purpose, because they alone were, in ordinary years, sufficiently dry. Such, to a great extent, were the lands in New England; and they were probably burned for more than 1,000 years."

This original open type forest is the direct antithesis of the present day type of "brush" or coppice wood which is characteristic of southern New England, and which is partly the result of clean cutting at frequent intervals. As the country was settled, much of the land was completely cleared and cultivated, mowed, or pastured. Many of the old records state that the colonists continued the burning of the woods after the expulsion of the Indians to maintain grass for pasturage in the areas not completely deforested. Progressive clearing of the land for agriculture continued until the early part of the nineteenth century. Between 1820 and 1850 the area of cleared land attained its maximum amounting to 75 or 80 per cent of the total in many southern New England counties. Since the Civil War, there has been a gradual abandonment of this cleared land in many places, and slow reversion to forest. During the seventies, the portable steam sawmill came in, and by the end of the nineteenth century, practically all of the remaining old woodland tracts had been cut. As a result of these two factors, approximately 60 per cent of southern New England is now brush land or young woods, either succeeding the older woods or invading land which was once cleared or cultivated. Woodland trees one hundred years old are scarce, and forests in which the dominant trees are several centuries old, as was the original condition, are practically non-existent.

What do the early commentaries say that would throw light on the original forest types in southern New England? Captain John Smith in his description of southern New England (1616) made the statement<sup>7</sup> "Oke is the chiefe wood." Morton (1632) in his list of trees of New England gives greatest prominence to oak, walnut (hickory), and chestnut. Wood (1634)

<sup>6</sup> Probably *Agrostis hyemalis* (Walt.) BSP.

<sup>7</sup> P. 16.



stated that the "chiefe and common timber for ordinary use is oake and walnut."<sup>8</sup> The latter author gives a description of the early forest which is quoted as follows, inasmuch as in addition to confirming Morton's account, it gives a better idea of the character of the woods: "The timber of the Countrey grows straight and tall, some trees being twenty, some thirty foot high, before they spread their branches; generally the trees be not very thicke, though there be many that will serve for mill posts, some beeing three foote and a halfe o're. And wheras it is generally conceived that the woods grow so thicke, that there is no more cleare ground than is hewed out by labour of man; it is nothing so; in many places, divers acres being cleare, so that one may ride a hunting in most places of the land, if he will venture himselfe for being lost; there is no underwood saving in swamps and low grounds . . . for it being the custome of the Indians to burn the wood in November, when the grass is withered, and leaves dryed, it consumes all the underwood and rubbish, which otherwise would over grow the country, making it unpassable, and spoil their much affected hunting; so that by this meanes in those places where the Indians inhabit, there is scarce a bush or bramble, or any cumbersome underwood to be seene in the more champion ground, small wood growing in these places where the fire could not come is preserved."

Southern New England,<sup>9</sup> except the mountains, was at the time of this narrative, very probably covered with oak-hickory and oak-chestnut on the uplands, while the sandy, so-called "Pine plains" were pitch pine. The climatic climax types (white pine, hemlock, maple, beech) largely composed of trees sensitive to fire, were very probably restricted to the moister areas or to protected ravines and gorges. The extensive annual fires to which the land was subjected for centuries would tend to make the xeric and fire-resistant oaks, the "chiefe wood." That the distribution of the white pine and hemlock in the region designated as the "white pine" area in Figure 1 and the hemlock type in the area in southern Connecticut mapped as the "oak" region, was greatly restricted until a comparatively recent date may be surmised from the following. As late as the beginning of the nineteenth century, Dwight (vol. IV, p. 218) states "that the pine, south of the district of Maine, if it were all collected into one spot, would scarcely cover the county of Hampshire" and that "nine-tenths of all the forests in this country, South of the District of Maine, are composed either of oak, hickory, etc., or of beach, maple, etc."

That most of southern New England was not typical forest, but a woodland greatly modified by fire and anthropic factors seems quite certain. In addition to keeping the woods open by means of fire, the Indians had undoubtedly cleared certain regions, either for their primitive agriculture or for other reasons. The present site of Boston was reported to have been so

<sup>8</sup> In the old accounts—"walnut" was used synonymously with hickory and does not refer to *Juglans*.

<sup>9</sup> Probably most of the southern New England region, except the Berkshire, Taconic and possibly the hilly region of North Central Massachusetts had been subjected to the fires set by the Indians.

free of forest, presumed to have been cleared by the Indians, that the settlers were forced to obtain their firewood from the wooded islands in the harbor. There were so-called "natural meadows" along many of the streams, and on many of the higher, overdrained sandy or gravelly knolls were open areas dominated by *Andropogon scoparius*, the climax grassland of such sites in southern New England. In addition, there were open brushy plains in certain regions, composed largely of bear oak (*Quercus ilicifolia* Wang.) and sweet fern (*Comptonia asplenifolia* L.), which were the habitats of the heath-hen. While many of these were no doubt kept in this condition by fire, there were undoubtedly others such as the Seekonk plain, in Bristol County, Massachusetts; and the Plainfield area in Windham County, Connecticut, which were edaphic and physiographically similar to the Hempstead plain of Long Island, New York (Harper, 1912). Many of the natural wet meadows may have originated as beaver meadows.

Wood (1634) described the natural meadows: "There be likewise in divers places neare the plantations great broad meadows, wherein grow neither shrub or tree, lying low, in which Plaines growes as much grasse, as may be throwne out with a sithe, thicke and long, as high as a man's middle."

The activities of other native animals may have been important in influencing the original vegetative types. The browsing of great numbers of deer (Rhoads, 1903), the effect of the feeding, roosting and nesting of the millions of wild pigeons (Lawson, 1709), and the great numbers of wild turkeys, both of which fed largely at certain seasons of the year, on acorns and beech mast, were influences which in certain regions may have locally modified the character of the forest.

Fires, in addition to reducing the undergrowth, must have exerted a profound influence on the forest types. Such fire-sensitive species as hemlock, white pine, beech, and juniper must have been greatly restricted in areas where they would otherwise have occurred in abundance. Many other trees as a result of the fire-scorching became hollow, and it is probable that the great number of hollow trees reported in the early woodlands may have owed their condition to this cause.

#### HISTORICAL FACTORS: THE POST-GLACIAL PERIOD

As the ice mass of the last glaciation slowly retreated from Long Island Sound, the wave of vegetation that followed in its wake undoubtedly roughly corresponded in its successive stages to those which may now be encountered from the tundra southward. It is reasonable to suppose that southern New England was at one time tundra, followed by the boreal forest of spruce and fir, relicts of which now exist on the highest mountains of the north-western and north-central parts. As climatic conditions became less favorable to this type, an invasion of white pine and hemlock very probably occurred and also an infiltration of maple and beech from the west.

As we do not as yet have pollen analyses of peat bogs from New England, we do not know exactly how or when one forest type succeeded another. It is known, however, that in the middle West, a dry period occurred about 3,000 years ago which resulted in a dominance of xeric species, principally oaks. Although there is no present evidence of such a period in southern New England, it is not unreasonable to suppose that such did occur and very probably was the basic reason for the establishment of oak and pitch pine forests which were maintained by the Indians' fires until the white occupancy.

It seems probable also that fires were frequent on dry sites, even before the Indian occupancy. Such fires could have been started by lightning igniting the dead wood in hollow trees which might burn for several days and from the sparks of which a general conflagration could have been kindled. It can safely be assumed that fire has been a constant attendant of dry woods from time immemorial.

#### HISTORICAL FACTORS: COLONIZATION

During the seventeenth century, white settlement was hampered by Indian hostility and warfare, but this factor once removed, colonization went on rapidly. By the middle of the eighteenth century, settlements existed in all of the present counties, and most of the present townships. The woodlands were completely cleared over large areas; while in others, cessation of the Indian fires had resulted in a heavy undergrowth. Other woodlands were still burned by the settlers to keep them open for grazing. In many places woods were completely cleared for pasturage. This was done by felling the larger trees in June and burning the tangled windrows when the leaves had dried in late July or August. As settlement progressed, more and more of the entire region was fenced in with stone fences, making a marked and abrupt division between woodlands, pastures, fields, and cultivated grounds.

Much of the wealth of the settlers lay in their cattle and sheep, and the intense grazing to which a large part of the region was subjected for over 150 years had a profound effect upon the vegetational types, as will be described later.

Exploitation of the woodlands kept pace with the agricultural development. During the latter part of the seventeenth century and the early part of the eighteenth, the pitch pine forests were worked for tar, turpentine, and lampblack, which were exported to Great Britain. Temple (1889) in his history of Palmer, Massachusetts, in describing the early settlement of the region, states that as a means of raising money, "these first-comers to the Elbow Tract made considerable turpentine and tar. The pitch pines, which were then the old growth on our plains, were 'boxed'," while "candlewood" was obtained from the pitchy knots.

Pitch pine was an important source of fuel for the colonists and later,

during the early half of the nineteenth century, great quantities were consumed for fuel by the wood-burning locomotives. Emerson (1846) states that "pitch pine is preferred to any other wood in the northern states as fuel for steam engines and vast quantities of it are also consumed for the supply of families." The estimated annual consumption by the Massachusetts railroads at that time was 53,710 cords, which was almost entirely pitch pine.

The oak and hickory woods were also, as at the present time, largely cut for fuel. The sprouting of these trees after cutting perpetuated the "sprout lot" of the farmers. Dwight in 1821 (Vol. I, p. 80) states "when a field of wood is, in the language of our farmers, cut clean, i.e., when every tree is cut down, so far as any progress is made, vigorous shoots sprout from every stump, and having their nourishment supplied by the roots of the former tree, grow with a thrift and rapidity never seen in stems derived from the seed. Good grounds will thus yield a growth, amply sufficient for fuel, once in fourteen years."

Where white pines occurred, these were prized above every other tree for masts. In fact, one of the early names for the white pine was "mast pine." Regarding restrictions on cutting this species, Belknap (1792) in his History of New Hampshire (Vol. III, p. 81) states that "before the revolution all white pines (excepting those growing in any township granted before the 21st of September 1722) were accounted the King's property, and heavy penalties were annexed to the cutting of them, without leave from the King's surveyor."

#### THE PRINCIPAL FOREST REGIONS

The preceding has dealt largely with the historical factors. This evidence may now be compared with what present day ecology offers.

For convenience, southern New England may be divided roughly into the following regions:

(1) The Oak Region, (2) The White Pine Region, and (3) The Northern Forest Region.

These terms are employed for simplification and do not imply that, for instance, the white pine region is solid white pine forest, but simply that the region mapped is characterized by an abundance of white pine. These regions, outlined in Figure 1, correspond, to a great extent to the classification adopted by the New England Section of the Society of American Foresters, except that they give Cape Cod a distinct classification, termed "Pine and Oak Region," while what the writer calls the "Northern Forest Region" is termed the "Spruce and Northern Hardwood Region."

Furthermore this classification does not imply that the terms refer to the climatic climax type for the region, the occurrence of which in each region will be discussed later.



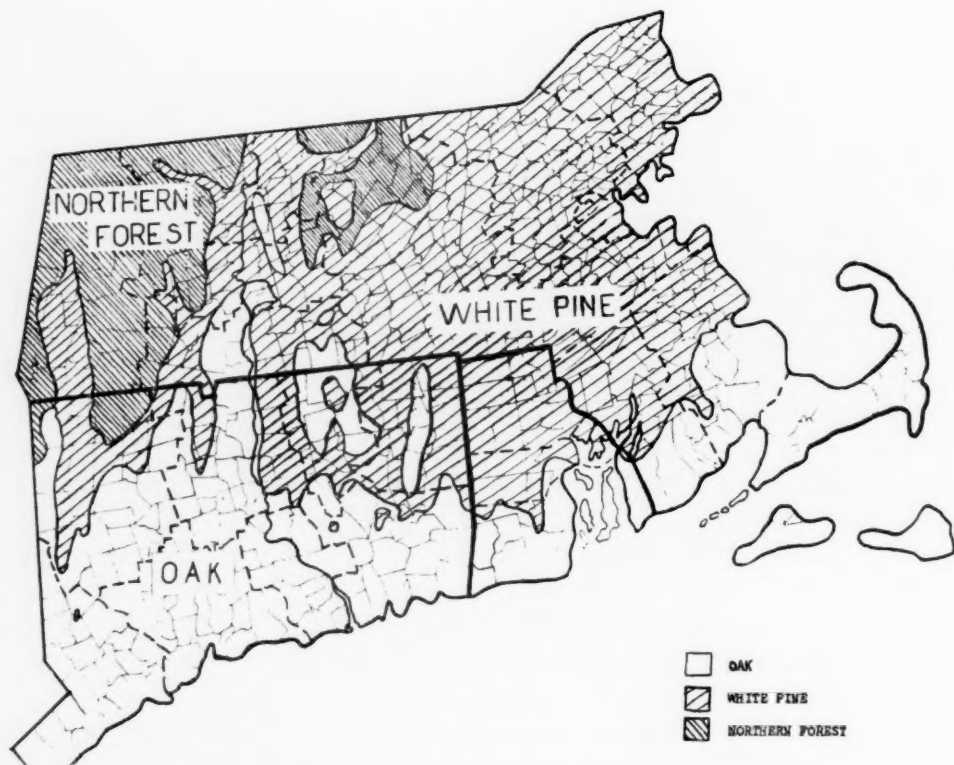


FIG. 1. The principal Forest Regions of southern New England. Approximate boundaries.

#### 1. THE OAK REGION

This occupies a large part of Connecticut, southern Rhode Island, and southeastern Massachusetts, and is characterized by the dominance of oaks and the absence or scarcity of white pine. Originally a large part of the better drained soil, land which was largely cleared for agriculture, was oak-hickory, while oak-chestnut predominated on the drier ridges and south slopes. The upper portions of the steeper ridges were undoubtedly, as they are today, characterized by chestnut oak (*Quercus montana* Willd.). The chestnut (*Castanea dentata* (Marsh.) Borkh.) has of course within the past twenty-five years been practically exterminated as a forest tree by the chestnut blight (*Endothia parasitica*). The swamps were largely red maple (*Acer rubrum* L.)—elm (American elm, *Ulmus americana* L.)—pin oak (*Quercus palustris* Muench.), the latter oak in southwestern Connecticut characteristically overtopping the forest. Swamp white oak (*Quercus bicolor* Willd.) was a component here also, while black gum (*Nyssa sylvatica* Marsh.) occurred in most of the swamps of the entire oak region. The principal oaks are the white (*Quercus alba* L.), black (*Quercus velutina* Lam.) and red (*Quercus rubra* L.); the two latter becoming less abundant in the eastern part where scarlet oak (*Quercus coccinea* Muench.) becomes numerous, par-



ticularly in southeastern Massachusetts where it is frequently the predominating species.

The lower better-drained soils arising from the swamps, and also the sheltered rocky ravines and north slopes were dominated by the typical mixed mesophytic forest (Figure 2), originally composed of oak, chestnut, hickory (*Carya ovata* (Mill.) K. Koch and *C. glabra* (Mill.) Spach.), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), tulip poplar (*Liriodendron tulipifera* L.), which characteristically overtopped the forest, and a varying admixture of eastern hemlock (*Tsuga canadensis* (L.) Carr.). This type probably represents the climatic climax of the region. Black or sweet birch (*Betula lenta* L.) is common in this type and where clean cutting occurs is apt to come in abundantly and form a secondary type together with an increase in oaks. In southwestern Connecticut, sweet gum (*Liquidambar styraciflua* L.) is an abundant component of the forest near the coast.

The successional types in this region have been very well worked out by Lutz (1928) who found that the common "old field" associations such as red cedar (*Juniperus virginiana* L.), gray birch (*Betula populifolia* Marsh.), pin cherry (*Prunus pennsylvanica* L.f.), choke cherry (*Prunus virginiana* L.), red maple, black birch and dogwood (*Cornus florida* L.) occurring in varying admixtures are succeeded by hardwoods, such as oak, hickory, white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.) and sugar maple, tending toward the hemlock-hardwood climax.

Succession on old fields and open land depends to a considerable extent on the site, and its relation to the position of light or wing-seeded trees. Gray birch is one of the first to come in as a rule, although abandoned upland mowings frequently show an abundance of choke cherry or pin cherry; lowland mowings revert to red maple or alder (*Alnus incana* (L.) Moench. and in some places *A. rugosa* (DuRoi) Spring). Pastures usually become heavily stocked with red cedar. Succession on cut-over lands may be further complicated by the occurrence of fire.

For many years, repeated "clean" cuttings favored chestnut, due to its outstanding ability to sprout and its rapid early growth, but the chestnut is now no longer important in forest ecology. There is a tendency for oaks to increase following cuttings, even in the mixed mesophytic types, which types, especially the hemlock associations, clean cutting practically destroys. Hemlock, although originally restricted by fires, occurred locally throughout southern New England, except possibly in the Cape Cod region, growing principally in ravines, gorges, north slopes and protected swamps and low moist sandy grounds. Theoretically it is the tree best fitted to dominate the climax forest of southern New England, due to its longevity, shade tolerance and ultimate size. On the other hand its susceptibility to fire and drying winds, and its rather high moisture requirements render it poorly adapted to

such xeric sites as south-exposed ridges and such sandy, level, wind-swept coastal regions as Cape Cod.

The Cape Cod region was originally partly oak forest on the better soils, pitch pine (*Pinus rigida* Mill.) on the lighter, sandy soils, and oak-pitch pine in the tension zone between the two. Dwight, 1821 (Vol. III, pp. 74-109) states that the woods from Wareham to Sandwich were of "yellow pine" with oaks interspersed at New Bedford and Rochester; from Orleans to Eastham, first "oaks," then "oak and pine" to Wellfleet and Truro. From Truro to Provincetown there were no woods but "whortleberry bushes and small oaks." From Sandwich to Plymouth were "yellow pine" plains. The region from Truro to Provincetown were originally wooded, to judge from Gosnold's account<sup>10</sup> "that the Pilgrims in 1620 found Cape Cod harbor compassed about to the very sea with oaks, pines, juniper, sassafras and other sweet wood." Nantucket was also reported to have been originally wooded with oak, hickory, pine and other trees (Chrysler, 1905). The complete destruction of forest in these places was due to cutting and grazing.

\* In northwestern Ohio, in the sandy regions near Lake Erie and western New York state in the Batavia region, were areas known as "oak openings," sandy areas supporting a scattered open growth of oaks intermingled with grass (*Andropogon scoparius*). A somewhat analogous condition exists on the sandy plains of North Haven, Connecticut, where there are areas of open sand. This condition has existed for a very long time. Dwight (1821) mentions it in his *Travels* (Vol. II, p. 30), stating that the soil "near the northern limit of the township is so light as in two or three places of small extent to be blown in drifts. In these places it is absolutely barren." (See Nichols, 1914.)

## 2. THE WHITE PINE REGION

This region is at present dominated by northern white pine (*Pinus strobus* L.) which although exceeded numerically by many other trees, is a striking feature of the landscape due to its height and evergreen appearance. The young trees are easily killed by fire and originally the species was undoubtedly much restricted by this factor. At the time of settlement it was probably abundant only in swamps; low, moist sandy areas (known as "pine flats"); and on exposed ridges. Where white pine occurs farther south in isolated stations in the oak region of southern New England, the sites are almost invariably exposed ridges, where competition with the more rapidly growing young hardwoods is less keen. Second growth stations of white pine in the oak region occur only where plantings have been made or where pastures or openings have seeded in from older trees, either planted or relicts on exposed areas.

The greater part of the area mapped as the white pine region was during

<sup>10</sup> Quoted in Freeman, F. *History of Cape Cod*, p. 62. Requested by Chrysler (1905).

the Indian occupation probably oak-hickory on the lower slopes and better drained uplands, and oak-chestnut on the drier ridges and slopes, with only scattered white pines or groups of white pines overtopping the woodland. Even the so-called "pine flats" were probably not pure white pine, but white pine with pitch pine or hemlock, or in the swamps, with red maple and yellow birch (*Betula lutea* Michx.) as an understory.

However, the great height of the white pine, with scattered trees dominating the forest, gave the impression of greater abundance than was really the case. The white pine was by far the tallest tree in the original New England forest, and so impressed the early travelers. Michaux stated that it was the loftiest and most valuable of the productions of the North American forest. "Its summit is seen at an immense distance, aspiring to heaven, far above the heads of the surrounding trees." Its size may have been exaggerated, although the largest trees were cut early in the history of the country and we have no definite method of ascertaining exactly the proportions which the white pine may have reached. At least we do not have today any white pines of 250 feet in height and 6 feet in diameter as recorded by Dwight (1821, Vol. I, p. 36) or 264 feet, as a Lancaster, New Hampshire, tree was reported to have been; or the trees at Blandford, Massachusetts, said by Emerson to have been 223 feet in height. Probably, however, some of the very large trees in the original forest reached a height of 200 feet. In 1841, a 90 foot mast from the Penobscot Valley in Maine measured 36 inches in diameter at the butt and 28 inches in diameter at the top. Michaux recorded two trunks near the banks of the Kennebec, "one of which was 154 feet in length and 54 inches in diameter; the other 142 feet in length and 44 inches in diameter."

An interesting portrayal of the white pine forest is given by Jeremy Belknap (1812, Vol. III, Chapter VI, p. 56). "Notwithstanding the gloomy appearance of an American forest, yet a contemplative mind may find in it many subjects of entertainment. The most obvious remark, is the silence which reigns through it. On a calm day, no sound is heard but that of running water, or perhaps the chirping of a squirrel or the squalling of a jay. Another thing, worthy of observation, is the aged and majestic appearance of the trees, of which the most notable is the mast pine. This tree often grows to the height of 150 and sometimes 200 feet. It is straight as an arrow, and has not branches but very near the top. It is from 20-40 inches in diameter at its base and appears like a stately pillar, adorned with a verdant capital in form of a cone. Interspersed among these are the common forest trees, of various kinds, whose height is generally about 60 or 80 feet. In swamps and near rivers, there is a thick growth of underwood, which renders traveling difficult. On higher lands, it is not so troublesome; and on dry plains it is quite inconsiderable."

An account of a pitch pine-white pine-hemlock forest is given by Wilson Flagg (1890, pp. 226 and 304). He speaks of the pitch pine thus: "Some of the ancient pine woods in New England were made up principally of this species. Such was that extensive wood near Concord, New Hampshire, known by the poetic appellation of 'Dark Plains,' and in the early part of the century occupying a wide, flat region in the valley of the Merrimack river." "I watched the scenes as we rode slowly by them,—the immense pillars that rose out of a level plain, strewed with brown foliage, and interspersed with a few bushes and straggling vines; the dark summits of the white pines that rose above the round heads of the other species which were the prevailing timber; the twilight that prevailed these woods even at high noon; and I thought of their seemingly boundless extent, of their mysterious solitude, and their unspeakable beauty."

While the two preceding descriptions refer to regions just outside that considered in the present work, they would undoubtedly apply to certain restricted areas in Massachusetts and northern Connecticut and Rhode Island encountered by the original settlers. Wood (1634) stated that he had "seene of these statly high groune trees, ten miles together, close by the River side, from which by shipping they might be conveyed to any desired port." Morton (1632) listed an "infinite store" of pine in "some parts of the country. I have traveled ten miles together where there is little or no other wood growing." Such might, however, have referred to pitch pine.

The climatic climax in this region is probably white pine-hemlock. The original extensiveness of the oak-chestnut-hickory pine type may have been due to the prevalence of fire, or it may have been even edaphic on the drier sites. The occurrence of white pine in the climax, despite its low tolerance of shade, may be explained on the basis of the following factors: 1. The enormous amount of seed that may be set by an individual tree. 2. The wide scattering of the winged seeds and its rapid growth in openings in the forest, caused by windthrows, or fires. 3. Its great height, normally overtopping the forest 10 to 40 feet or more. 4. Its rapid growth, upward through gaps in the forest canopy in an open woodland. Once above the foresty canopy its position is secure. 5. Its longevity. Spaulding records white pine 400 years old. 6. The crashing of the aged trees, opening up spaces in the forest. 7. The greater ability to withstand ice storms and heavy snows which are more destructive to oaks and other hardwoods.

The present abundance of pure white pine stands in this region is due largely, as stated by Dana (1930), to its ability to take possession of abandoned farm lands. When these pure stands are cut clean, as they generally are after 30 or 40 years, they revert to a secondary type of deciduous trees in varying proportions, unless pastured. When pastured, white pine generally becomes reestablished, if there are neighboring seed trees. As the prin-



cial monetary value of the southern New England woodland lies in white pine<sup>11</sup> for lumber, and oak and birch for fuel, they are so managed. In the oak and birch types of woodland there is a regeneration due to sprouting, unless pastured; in the white pine stands, regeneration *does not* take place, *unless pastured*. Cleared pastures in this region almost invariably revert to white pine or gray birch, both trees frequently becoming established while pasturing is continued. Old fields are occupied by the same species, although on overdrained and sandy sites pitch pine or aspens are frequently the pioneers. Where pasturing does not occur, the grass *Andropogon scoparius*, a species quickly destroyed by grazing, has a tendency to dominate in such sites and produces a "prairie" (see photo by Nichols, 1914, p. 188), which greatly delays reforestation, particularly if burned. In meadows and low mowings, red maple and alder are likely to be abundant, although white pines will frequently become established and eventually dominate the stand.

Where an old white pine-hemlock forest has been cut clean, this type is succeeded by a mixture of such trees as sugar maple, white ash, basswood, yellow and other birches, particularly in the northern part of the region. In the southern part, oaks are more likely to come in, particularly where the stand has been largely white pine. In many cases an understory of young oaks becomes established in a white pine grove, before cutting of the pine, and is thus ready to take its place when the pine is removed. The following observations were made on such a grove at Southbridge, Massachusetts.

- 1910. A grove of white pines about 70 years old which had evidently seeded in from an old "cabbage" pine in the corner of the lot, about 130 years old. Most of the trees were 70 to 80 feet high and 20 to 36 inches in diameter. Fifty or 60 years before, this grove was evidently surrounded by pasture or meadow land. The floor of the woodland had been burned over repeatedly producing a grassy condition.
- 1911. Fires ceased.
- 1912. Young "brush" mowed out by scythe.
- 1915. Canada mayflower, false solomon seal, solomon seal and other herbaceous plants in great profusion; asters and golden rod in the autumn.
- 1918. An undergrowth of oaks 2 to 5 feet high. Fire scars still present on some of the pines.
- 1928. Heavy oak undergrowth 5 to 20 feet high. Thick oak and pine leaf litter, obliterating grass and herbage which was characteristic

<sup>11</sup> A small group of sentinel pines, the tallest and oldest white pines in the locality, towering high above a woodlot overlooking the Quinnebaug valley near the Massachusetts-Connecticut line at Dudley, Massachusetts, had been a prominent land mark since the memory of the oldest inhabitants. These trees, previously estimated, ranged from 100 to 125 feet in height. The woodlot in which they occurred was cut in the autumn of 1931, and on May 22, 1932, diameters and ring counts of some of the larger stumps, which had been cut about a foot from the ground, were: 48 inches, 198 rings; 41 inches, 191 rings; 36 inches, 173 rings; 39 inches, 157 rings. Contrast with this, a white pine stump in the fire-swept Douglas woods, described later. This stump, a foot from the ground, measured 20 inches in diameter and showed 151 rings.



a dozen or more years previous. The old fire scars on the pines practically overgrown in most cases.

### 3. THE NORTHERN FOREST REGION

In the mountainous areas of western and north central Massachusetts, a type quite different from the preceding occurs. Although white pine is occasional and hemlock abundant, the bulk of the forest is what is known to foresters as the northern hardwood type, consisting largely of yellow birch, white birch, sugar maple and beech; with white ash and basswood abundant in certain areas. Originally the physiographic areas were very well marked and no doubt corresponded to the condition in Vermont which was classified by Thompson (1824, p. 26):

1. Alluvial areas—oak, butternut, elm, walnut (hickory), chestnut.
2. Higher flats—"Pine."
3. Medium uplands—Sugar maple, beech, birch, ash, basswood, elm, butternut, cherry, hornbeam, spruce, hemlock.
4. Sides and summits of mountains—Hemlock, spruce, fir.

Intensive cutting as well as other factors incidental to settling greatly disturbed the original condition. Cutting as usual destroyed the conifers. Second growth stands are apt to be characterized by a greater per cent of yellow birch, white birch, striped maple, pin cherry, and aspen than the original.

On the higher altitudes, red spruce and balsam fir predominate and originally formed nearly pure stands with a characteristic undergrowth of moosewood and hobblebush. Clean cutting throughout the area generally results in the possession of the land by northern hardwoods, particularly birch; while the old pastures and abandoned fields revert to conifers. Annual fires probably did not occur in this region as was the case farther south, although occasional fires in dry seasons occurred, destroying the spruce-fir types over large areas and initiating the succession of fireweeds, aspen, pin cherry and birch with eventually the conifers again invading and finally dominating.

In this region the climatic climax types were undoubtedly the spruce-fir (Fig. 2) on the higher altitudes, and hemlock-hardwoods of the type described by Lutz (1928) on the lower slopes. A virgin forest, the last of its kind in Connecticut, occurring at Colebrook until 1912 when it was cut, was undoubtedly of the latter type and represented the climax which at one time probably clothed the greater part of the Berkshire hills. Fortunately an accurate census of this tract was made by Nichols (1913) before it was destroyed. To quote Lutz's summarization, it was "characterized by the predominance of hemlock and beech. On the whole these two species were about equally abundant and taken together, comprised at least 55 per cent of the stand. The relative proportions of the two were found to vary, but almost

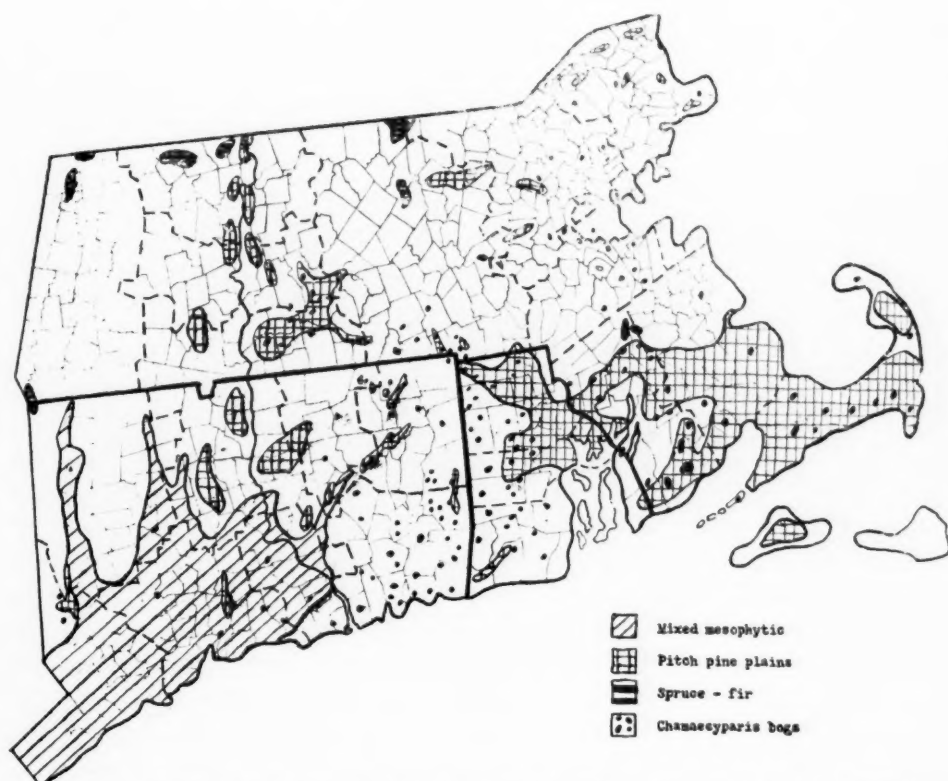


FIG. 2. Locations of certain forest types in southern New England. Approximate boundaries.

without exception one or the other was dominant. The remainder of the forest was made up approximately as follows (in per cent of the total number of trees): sugar maple, 12; yellow birch, 10; red oak, 6; chestnut, 6; white ash and basswood, 7; black cherry (*Prunus serotina* Ehrh.), red maple, black birch, and white pine, 4." Beech-maple, pure sugar maple stands and spruce-hardwoods, as physiographic climaxes, undoubtedly originally occurred in places, the two former on the drier upper slopes or tops of the lower hills and plateaus, and the latter in the tension zone between the spruce-fir of the higher altitudes and the hemlock-hardwoods of the moist slopes. On overdrained dry ridges, oaks and chestnut also occurred.

#### CERTAIN PHYSIOGRAPHIC TYPES IN NEW ENGLAND

##### 1. Flood Plain and Alluvial Woodland Associations.

A characteristic flood plain association occurred along most of the larger streams in southern New England, more extensive probably along certain portions of the Connecticut and Housatonic rivers than elsewhere. American elm and sycamore (*Platanus occidentalis* L.) were general, with silver maple (*Acer saccharinum* L.) and red maple abundant in some places. River birch (*Betula nigra* L.) was local and scarce as was also hackberry (*Celtis occi-*

*dentalis* L.). The sand bars and sandy banks were dominated by cottonwood (*Populus deltoides* Marsh.) and willow (*Salix* spp.).

Edaphic meadows, some of which were of great extent, also occurred in the river valleys and were known as Intervales. According to Dwight, these were most extensive at "Wethersfield, Hartford, Windsor, Glastonberry, East Hartford, and East Windsor in Connecticut; Longmeadow, Springfield, Northampton, Hadly, Hatfield, Sunderland, Deerfield and Northfield in Massachusetts." Brimfield and Brookfield, Massachusetts, both had extensive natural meadows.

Great woodlands also occurred on the alluvial soils and were composed of many of the species listed above with a greater admixture of red oak, chestnut, hickory, white ash and particularly butternut (*Juglans cinerea* L.). In the white pine region, this pine was also an abundant component of the alluvial forest.

## 2. Pine Plains.

The pine plains (Fig. 2) so frequently mentioned by the early writers were for the most part composed of pitch pine, although in the white pine region there tended to be an admixture of white pine and even hemlock, particularly in the lower moister areas. In the southern and southeastern parts there was a tendency to oaks, particularly scarlet, white and black. The pine plains were invariably on light, sandy soil. The abundance of pitch pine was probably due to the frequency of fire which favored this fire-resistant species by destroying the humus and eliminating competing species. With the fire factor removed, there is a tendency for white pine and hemlock to supplant the pitch pine in the northern area, and for oak or pitch pine and oak to dominate on these plains in the southern part. The pitch pine forests were early exploited and disappeared over a considerable portion of their original range. Cutting is particularly disastrous to conifers, due to the inability of most to sprout, and the cutting of the pitch pine woods almost invariably resulted in a replacement by oak. Dwight (1821, Letter XXXI, p. 39) observed "From Windsor the road, leaving the Connecticut River proceeds to Suffield over a plain of yellow pines, about five miles in extent. At the entrance upon this plain, the pines for near a mile were, many years since, entirely cut off: and in their place has sprung up a forest of oaks." He also spoke of Montague, Hatfield, Ware, Ludlow, Palmer, Sandwich and Plymouth, Massachusetts, as being characterized by extensive "yellow" pine plains. Letter L, p. 2, stated "Immediately after we left Plymouth we ascended the brow of a vast, yellow pine plain, spreading over the greater part of the county of Plymouth, a part of the county of Bristol and a part of the state of Rhode Island."

Some of the higher over-drained gravelly plains were, however, destitute of large trees from the earliest times. The difficulties of the early settlers at Concord, Massachusetts in 1635 were described in Johnson's "Wonder-work-

ing Providence" (Barber, 1848, p. 378). Much of the land was composed of "ragged plains," largely "shrub oak" and sweetfern, making traveling very difficult.

### 3. *Chamaecyparis* Bogs.

Scattered peat bogs bearing a growth of southern or coast white cedar (*Chamaecyparis thyoides* (L.) BSP.) occur through the southern and eastern area of southern New England, invading stagnant pools and lakes (Fig. 2). Particularly in the more northerly located bogs, there is a fringe of tamarack (*Larix laricina* (Du Roi) Koch.) and black spruce (*Picea mariana* (Mill.) BSP.) at the edge of the water, the thick growth of cedar supplanting this type farther back. The *Chamaecyparis* is undoubtedly an evanescent type, being succeeded, as the swamps dry out, by the deciduous swamp forest in the oak region, and by white pine-hemlock in the white pine region. Clean cutting completely destroys the cedar type, red maple and yellow birch succeeding it. Sphagnum moss, pitcher plant (*Sarracenia purpurea* L.) and poison sumac (*Rhus vernix* L.) are common associates in the more open spots, with *Caltha palustris* growing in the shaded pools. In southeastern Connecticut, there is frequently a heavy undergrowth of *Rhododendron maximum*.

### 4. Maple Swamps.

Most of the swamps in southern New England are characterized by the presence of red maple. While there were undoubtedly many maple swamps originally, it is probable that most of those at the present time represent a secondary condition. The cutting of the white pine and hemlock in the swamps of the white pine region has left the red maple and yellow birch to occupy the site sometimes to the complete exclusion of the original dominant species; while in the oak region, the swamps which are now red maple, black gum (*Nyssa sylvatica* Marsh.) and elm, undoubtedly contained much more pin oak than occurs today. In old growth swamps in this region the pin oak almost invariably overtops the elm and maple, while the swamp white oak was also a dominant species. Probably the oaks and the white ash dominated the better sites, restricting the pure stands of elm and maple to the least drained situations.

### EFFECTS OF PASTURING

Two centuries of pasturing have had a profound effect upon the vegetation of southern New England, although the country is not nearly so extensively pastured as it was 75 or 100 years ago. At that time the pastures were largely kept cleared of "brush" by means of the scythe and "grub hoe." This brush was composed principally of shrubs or young trees of species distasteful to cattle. As stock raising waned, many of the pastures were left idle and allowed to revert to brush and forest. In the white pine region, this became profitable to the farmer, who was able to realize on the young white



pine timber which quickly took possession of such sites. The larger trees coming in on pastured land in New England are almost invariably conifers. As a rule these are not browsed by cattle. The destruction of the young hardwoods by grazing has thus, by eliminating competition, favored the conifers.

In many parts of the oak region, particularly in western Connecticut where the soil is less acid, red cedar is an abundant invader of pastures. Originally, due to its low tolerance of shade, slow growth, and susceptibility to fire, this species was confined to exposed rocky ridges, protected open borders of swamps and along the seacoast. In the white pine region, the white pine frequently forms pure stands on pasture sites, while in the northern forest region where spruce and fir occur, these species are most likely to reclaim pastures on the higher land. In hilly regions, pure stands of hemlock frequently claim protected, pastured, north slopes; while in sandy regions, the pitch pine is a frequent pioneer. East of the Connecticut River, the patches of *Juniperus communis* are frequently indicative of former sheep grazing.

Probably the original grassland on the higher sandy or gravelly sites was almost pure *Andropogon scoparius*. This species is destroyed by grazing, its place being taken by shorter grasses. If grazing is abandoned, *A. scoparius* quickly becomes reestablished. Along railroad rights-of-way which are frequently burned, *Andropogon scoparius* is the dominant grass.

Among the shrubs and small trees invading pasture land, may be mentioned the gray birch, which is abundant throughout southern New England, as well as species of *Vaccinium* sp., *Rhus* sp., and *Myrica* sp. *Comptonia asplenifolia*, *Juniperus communis*, and *Baptisia tinctoria* which are abundant pasture species in many localities east of the Connecticut River, while *Potentilla fruticosa* may spread over moist pastures on the higher lands of the Berkshire and Taconic ranges.

#### EXAMPLES OF OLD-GROWTH FOREST

##### 1. Oak Region.

It seemed an almost impossible task to locate any woodland of even very limited extent which would at all approach original conditions. I eventually found a small tract near Stamford, Connecticut, which because of its proximity to a railroad had been burned over annually for a great many years, was not subject to grazing, and the trees were of relatively great age. Black oak, white oak, hickory, and sweet gum dominated and stood far apart. Flowering dogwood formed a scattered understory. There was no underbrush. A ring count on an oak stump showed somewhat over 200 years. Evidently the trees were old, but due to the dry site and prevalence of fires had grown slowly. The larger trees were 60 to 75 feet in height. Many were hollow or showed extensive fire scars. This was particularly true of the few beech, maple, elm, and pin oak which existed in the grove. The other oaks and hickories as a rule did not show fire scars (Figs. 3 and 4).



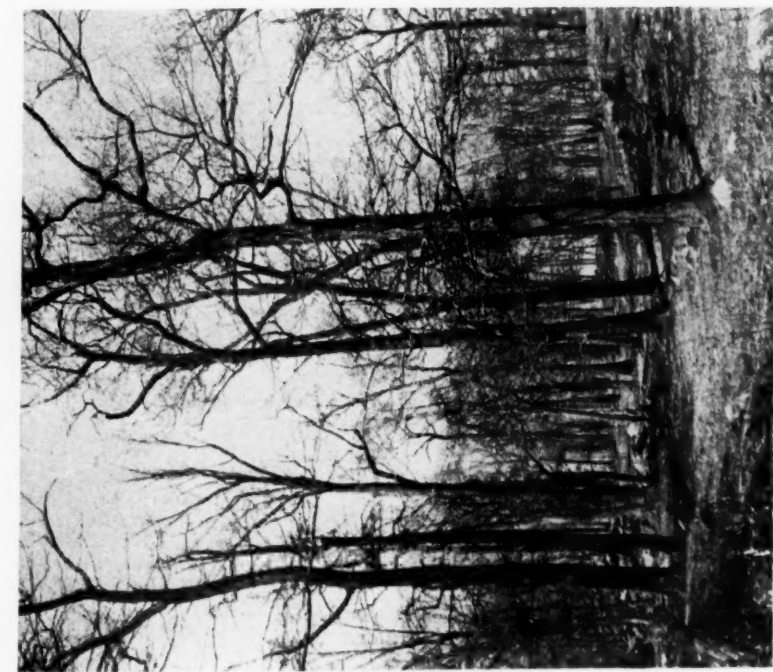


FIG. 3. Oak-hickory woodland, Stamford, Connecticut, subject to annual fires, resulting in an open stand free from underbrush.

(Photo by Dr. R. P. Marshall)

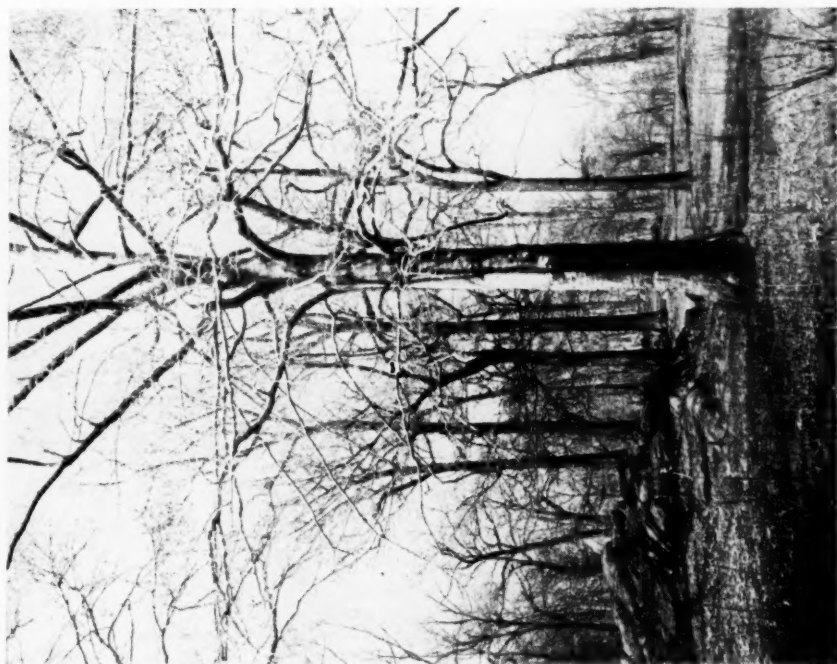


FIG. 4. Same grove as in Fig. 3, showing fire scars on beech. The ground cover near the ledge is largely *Dicentra cucullaria* (L.) Bernh.

(Photo by Dr. R. P. Marshall)

In direct contrast to this grove was an original hardwood grove north of Stamford, which had probably not been pastured for many years (Fig. 5). The trees were much larger and the average age may have been slightly greater. Although the large trees stood far apart, there was a dense undergrowth of sweet birch, *Cornus florida*, *Viburnum*, greenbrier (*Smilax* sp.) and others. Fires had only rarely occurred as evidenced by the dense undergrowth. This grove shows an interesting transition from swamp to upland condition; that is from the swamp type with pin oak, red maple and elm, through mixed mesophytic beech, sugar maple, oak, and tulip poplar (the latter overtopping the forest) to oak-hickory on the higher ground and oak-chestnut (the latter now dead) on the steep, drier slope. There is no hemlock in this grove.

At Laddin Rock, near Stamford, is an old grove of hemlock and mixed mesophytic woodland (Fig. 6). This is in a protected ravine and many of the trees are 200 years or more old.

## 2. White Pine Region.

An interesting old tract, formerly occurring in this region and known as the Lawson lot, was located near the Woodstock-Union township line in Connecticut. Largely white pine-hemlock, a very interesting transition was shown from swamp to high dry ridge. This grove was dominated by white pine, whose crests overtopped the rest of the forest ten to forty feet, their jagged crowns outlined against the horizon, producing a landmark recognizable for miles around. The swamp sites were largely forested with white pine, hemlock, yellow birch, red maple, and elm. Large sugar maples and red oaks were scattered through the grove on the slightly higher ground; while chestnut, red oak, black oak, white oak, and sweet birch occurred on the higher, drier slopes. White pine was omnipresent; the hemlocks were everywhere also but most numerous in the ravines. This was a wild-appearing woodland. Local inhabitants claimed it to be original forest. There were no signs of fire, pasturing, or cutting. The forest floor was spongy with vegetational debris, and windthrown trees extended their great lengths along the ground. Moss-grown and lichen-covered trunks of standing trees gave the impression of great age, while on the lower slopes great banks of mountain laurel 7 to 15 feet high added to the wildness of the scene. The writer first visited this region in 1917. It was a windy April day and in travelling through the woodland, one was impressed by the fact that although it appeared calm down in the woods, the tops of the great pines were swaying, and the silence was broken by the creaking and groaning of rubbing branches and the roar of the wind through the evergreen tops. The writer was unable to make accurate estimates of the heights of the trees, although he suspected that some of the taller pines may have been 120 feet in height, some of the hemlocks exceeded 90, while the average height of the oaks and chestnuts was

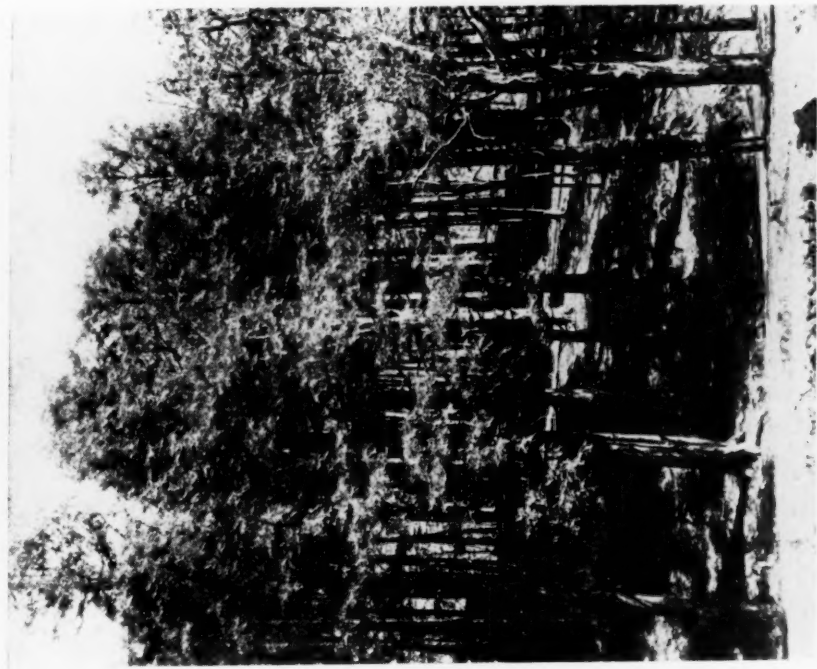


FIG. 6. Laddin Rock near Stamford, Connecticut; Hemlock grove in mixed mesophytic woodland. The deciduous tree in the right foreground is a red maple. A few beech are discernible in the grove. Undergrowth has probably been artificially removed. The tallest hemlock in the foreground is about 100 feet in height.  
(Photo by Dr. R. P. Marshall)



FIG. 5. Oak-hickory woodland, Stamford, Connecticut, not subject to frequent fires. The large trees stand far apart but there is a dense undergrowth. The black oak in the foreground is 114 feet in height.  
(Photo by Dr. R. P. Marshall)

70 to 80 feet. The trees of largest diameter were red oaks and chestnuts, some of the latter being nearly 5 feet through the trunk near the base. The young growth was largely hemlock. This led the writer to suspect that the predominance of the evergreens might have been a recent development, and that in colonial times the area might have been an open oak-chestnut woodland, particularly as in a part of the woods which had just been felled, it was impossible to find a pine stump showing more than 150 rings. Some of the oaks were over 200. This whole region was cut over a few years after the World War, and every vestige of the conifers destroyed. When the area was revisited in 1931, the predominating trees of the second growth were birch and sugar maple. The latter had seeded in from old maples which had been left standing. A few years prior to cutting, most of the chestnuts had succumbed to the blight.

A somewhat similar tract, in which the pines are much older and larger, is a white pine-hemlock grove at Cornwall, Connecticut, known as the Cathedral Pines (Figs. 7 and 8). Scattered through this grove are large beech, red oak, and sugar maple. There are also chestnuts, but these have now been killed by the blight. The tallest pines here are about 140 feet in height, and judging by the number of rings on a windfall, some of them may be 200 to 300 years old.

The so-called Gulf woods near Southbridge, Massachusetts, long since cut off, were, according to local tradition, largely white pine, hemlock, with here and there large oaks, chestnuts, and beech trees.

The famous Douglas woods, a large tract between Douglas and Webster, Massachusetts, lying on sterile rocky ground, has been cut over at frequent intervals and is now largely low "brush" of young scarlet oak, black oak, and white oak sprouts. Twenty years ago there was considerable chestnut and when I visited the region in 1916, in a tract where the woods seemed the oldest, white, scarlet, and black oaks predominated with scattered white pine and chestnut; and considerable pitch pine in the sandier areas. The swamps were largely white pine, red maple, and yellow birch, with several *chamaecyparis* bogs. This is still a fire-swept area. At the writer's first visit, he thought that originally it may have been predominantly white pine and hemlock, and that frequent fires and repeated cutting had contributed to the destruction of this type. However, the Indians' fires had undoubtedly swept the region long before white settlement and it is probable that in colonial days the distribution of the various forest trees did not differ greatly from that of the present time. Dwight visited the region in the latter part of the eighteenth century and to quote his account: "In the Southwestern part of this township is a large tract of forest known by the name of the Douglas Woods. The trees which are of oak, chestnut, etc., are of moderate size and prove the soil to be indifferent. In the year 1805, when I passed through this



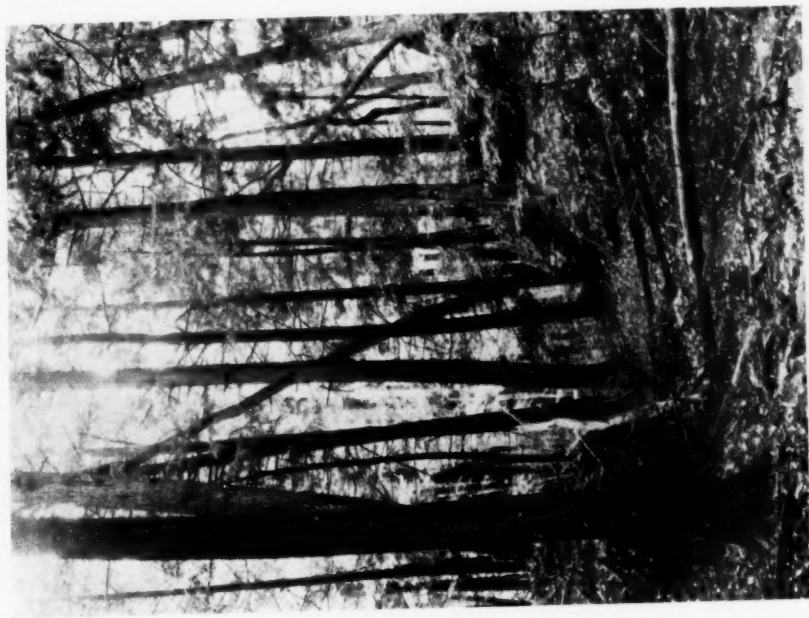


FIG. 8. Hemlock ravine in same grove as Fig. 3. The tallest hemlocks are about 100 feet tall.

(Photo by Dr. R. B. Gordon)

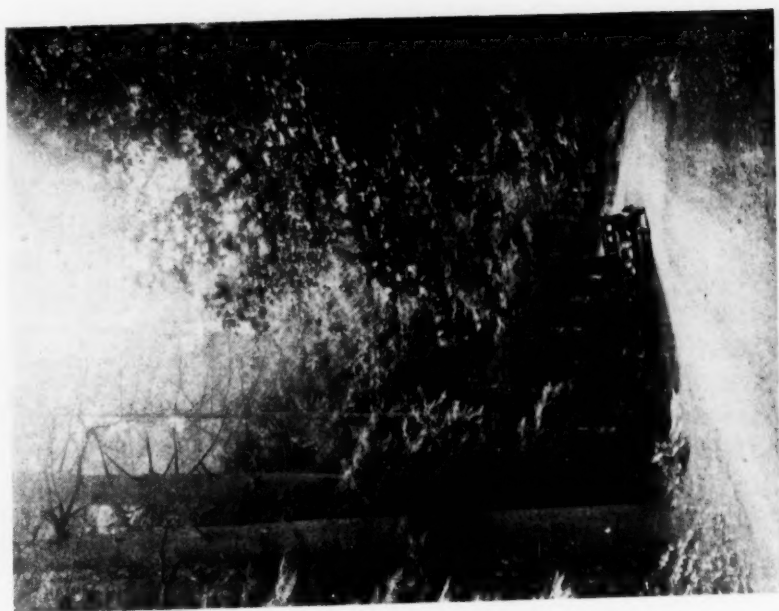


FIG. 7. White pine-hemlock at Cornwall, Connecticut. The tallest white pines are about 140 feet in height.

(Photo by Dr. R. B. Gordon)



region again, I perceived that the inhabitants had begun to make serious depredations on this tract." Dwight's route through the Douglas woods was the old Boston-Hartford stage road from Douglas to East Thompson. Due to repeated cuttings at frequent intervals, this particular part of the region is now largely scarlet oak and bear oak scrub. In the very few relict patches of old trees, the undergrowth on the drier sites is slight and composed mostly of low species of *Vaccinium*.

At South Pond near Brookfield, Massachusetts, on a sandy bluff extending into the lake, known as the Point of Pines, is a very interesting bit of woodland. When I first visited the spot in 1918, the blight had not yet killed the chestnuts, which were the most massive trees scattered through the grove. There were a number of white and red oaks of considerable size and age while scattered white pines, one of which was considerably over 100 feet in height, overtopped the stand. There were a number of very tall pitch pines also, 80 to 90 feet high, but most of the understory was composed of hemlocks of varying ages. The cleared land and pasture east of the grove had seeded in heavily to white pine, with a few of the more sandy spots to pitch pine.

### 3. The Northern Forest.

A beautiful example of the northern forest still exists in the State Park at Mt. Graylock in the northwestern corner of Massachusetts. The spruce-fir forest is in a natural condition and is one of the most strikingly beautiful groves left in Massachusetts. The grove referred to is that which occurs on the west side of the peak, on the upper slope at the camping ground toward the "Hopper." Most of the stand is red spruce. Balsam fir, canoe birch and a scattering of other northern hardwoods also occur. The trees are tall and straight and give the impression of great age. Some of the taller spruces may be 90 feet or over in height. The undergrowth is rather sparse and is largely hobble bush and striped maple.

### AGES OF FOREST TREES IN THIS AREA

Oaks are noted for their longevity, but it is doubtful whether any of our species, even if allowed to live, would attain the age (the proverbial 900 years) of European species. The white oak probably reached the greatest age of our trees under original conditions. The famous Charter Oak at Hartford, Connecticut, presumably a white oak, destroyed by a windstorm on August 21, 1856, was estimated as 1,000 years old, but as it was hollow and no accurate ring count could have been made, this estimate is no more than a guess. *The New England Farmer* (Vol. IV, p. 242) in 1826 recorded its girth at the ground as 36 feet, making it easily the largest oak of which we have record in New England. Sycamores attain a relatively great age, and the large tree at Sunderland, Mass., has been estimated as 500 years of

age.<sup>12</sup> Probably hemlock commonly attains the greatest age of our forest trees. A tree cut on the Holyoke range in 1922 showed over 400 rings. Frothingham (1915) reports hemlocks of 500 to 600 years old. The white pine although a relatively long-lived tree, probably did not ordinarily attain this age. Trees 400 years old have been recorded.<sup>13</sup> One of the oldest white pines in southern New England was the famous "Bear Tree" in Palmer, Massachusetts. This tree was cut about 1921. When I saw it in 1919 it was hollow and badly infested with carpenter ants. I described it in my notes as a triple-leader tree, branching about 20 feet from the ground, 100 feet in height, and about 5½ feet in diameter at the base. It gained its name from the tradition that in the days of early settlement, about 175 years before, a black bear was shot out of the lower branches.

Some specimens of *Chamaecyparis thyoides* in the cedar bogs were reported to be old. Their growth in most cases is extremely slow. At the cedar swamp in Charlton, Mass., a tree about 35 feet in height and a foot in diameter showed 148 rings. The chestnut was a rapidly growing, but comparatively short-lived tree.<sup>14</sup> The largest stump which I found in southern New England, although 75 inches in diameter a foot from the ground, showed only 250 rings.

#### PRESENT DAY TENDENCIES

As the white pine-hemlock was the most striking and spectacular type in southern New England, it is deplorable that old stands could not have been preserved here and there. It would seem advisable to foster this type on reservations, estates, and in state forests, particularly in the white pine region. Although reproduction of white pine is abundant here, the high value of this tree for lumber leads to cutting it as soon as merchantable size is reached. There are many sites, however, even now where young white pines 50 to 80 years of age are associated with hemlocks and other trees in a proportion similar to the old groves, and if some of these could be saved and natural conditions preserved for a century or two, some of the aged and impressive appearance of the climax forest could be attained.

The value of the white pine is leading more and more to its culture in the white pine region. Fields and pastures are allowed to seed in. Attempts are made by owners to increase their acreage of pine. The value of hardwood groves lies in their fuel production, and when cuttings are made for this purpose, the scattered pines are usually spared with a view to their increase. Many sites are known which have been transformed from pine-hardwood to predominately pine in the past 15 years by simply removing the hardwoods

<sup>12</sup> In 1929 recorded as 24 feet 3 inches in circumference at the base and over 100 feet high.

<sup>13</sup> Spaulding (1899) records (p. 27) a white pine in Michigan, 48 inches in diameter breast high, 170 feet in height and 460 years old.

<sup>14</sup> Chestnut is frequently struck by lightning and many of the large old trees of 25 years ago showed the effect of lightning strokes. Probably the death of many of the larger older trees was hastened by this cause.

for fuel. There has been considerable planting of white pine with many thrifty young stands resulting, although some of these outside the white pine region have not been preëminently successful. The hazard of fire so destructive to young white pine is an ever-present menace to the white pine. During the past 25 years there has been a definite movement towards the protection of woodlands for aesthetic purposes, in the increase of state forests, state parks, reservations and estates.

Chestnut groves were fostered until the blight destroyed the species. The place of the chestnut in the forest is now being taken by other trees, principally oaks.

#### LITERATURE CITED

- Averill, R. C., W. B. Averill, and W. J. Stephens. 1923. A Statistical Forest Survey of Seven Towns in Central Massachusetts. Harvard Forest Bul. 6.
- Barber, J. 1838. History of Connecticut.  
1848. History of Massachusetts.
- Belknap, Jeremy. 1792. History of New Hampshire. 3: 56 and 81.
- Bidwell, P. W., and J. J. Falconer. 1925. History of Agriculture in Northern United States. Carnegie Institute Pub. 358.
- Chase, L. B. 1925. The Bay Path and Along the Way.
- Chrysler, M. A. 1905. Reforestation at Woods Hole, Massachusetts. A Study in Succession. Rhodora, 7: 121-129.
- Clements, F. E. 1916. Plant Succession. Carnegie Institute Pub. 242.
- Dana, S. T. 1930. Timber growing and Logging practice in the Northeast. U. S. Dept. Agr. Tech. Bul. 166.
- Dwight, Timothy. 1821. Travels in New England and New York. 4 vols.
- Emerson, G. B. 1846. A Report on the Trees and Shrubs growing Naturally in the Forests of Massachusetts. p. 70.
- Flagg, Wilson. 1890. A Year among the Trees. Pp. 226 and 304.
- Freeland. 1894. Records of Oxford, Massachusetts.
- Frothingham, E. H. 1912. The Second-growth Hardwoods in Connecticut. U. S. D. A., Forest Service Bul. 96.  
1915. The Eastern Hemlock. U. S. Dept. Agri. Bul. 152.
- Harper, R. M. 1912. The Hempstead Plains of Long Island. Torreyia 12: 277-286.  
1912. The Diverse Habitats of the Eastern Red Cedar and their Interpretation. Torreyia 12: 7.
- Hawes, A. F., and R. C. Hawley. 1909. Forest Survey of Litchfield and New Haven Counties, Connecticut. Conn. Agri. Exp. Sta. Bul. 162.
- Hickock, H. W., M. F. Morgan, H. J. Lutz, Henry Bull, and H. A. Lunt. 1931. The Relation of Forest Composition and Rate of Growth to Certain Soil Characters. Conn. Agri. Exp. Sta. Bul. 330.
- Jenkins, Stephen. 1914. The Old Boston Post Road.
- Josselyn, John. 1672. New England's Rarities.  
1675. Two Voyages to New England.
- Korstian, C. F., and W. D. Brush. 1931. The Southern White Cedar. U. S. Dept. Agri. Tech. Bul. 251.

- Korstian, C. F., and P. W. Stickel.** 1927. The Natural Replacement of Blight-killed Chestnut in the Hardwood Forest of the Northeast. Jour. Agri. Res. **34**: 631-648.  
1927. The Natural Replacement of Blight-killed Chestnut. U. S. Dept. Agri. Misc. Circ. 100.
- Latimer, W. J., and M. O. Lanphear.** Soil Survey of Essex County, Mass. U. S. Dept. Agri. Bur. Chem. and Soils, No. 14, Series 1925.  
Soil Survey of Middlesex County, Mass. U. S. Dept. Agri. Bur. Chem. and Soils, No. 26, Series 1924.  
1929. Soil Survey of Berkshire County, Mass. U. S. Dept. Agri. Bur. Chem. and Soils, No. 39. Series 1923.
- Latimer, W. J., R. F. R. Martin, and M. O. Lanphear.** 1927. Soil Survey of Worcester County, Mass. U. S. Dept. Agri. Bur. of Soils.
- Latimer, W. J., E. T. Maxon, H. C. Smith, A. S. Mallory, and O. H. Roberts.** 1924. Soil Survey of Norfolk, Bristol and Barnstable Counties, Mass. U. S. Dept. Agri. Bur. of Soils.
- Lawson, John.** 1709. History of Carolina and Audubon's account of the pigeon roost on the banks of the Green River in Kentucky.
- Lawson, H. M.** 1893. The History of Union, Connecticut.
- Love, W. D.** 1914. The Colonial History of Hartford.
- Lutz, H. J.** 1928. Trends and Silvicultural Significance of Upland Forest Successions in Southern New England. Yale Univ. School of Forestry Bul. 22.
- Merrill, P. H., and R. C. Hawley.** 1924. Hemlock: Its place in the Silviculture of the Southern New England Forest. Yale Univ. School of Forestry Bul. 12.
- Moore, B., H. M. Richards, H. A. Gleason, and A. B. Stout.** 1924. Hemlock and its Environment. I. Field Records. Bul. New York Bot. Garden **12**: 325-350.
- Morgan, M. F.** 1930. The Soils of Connecticut. Conn. Agri. Exp. Sta. Bul. 320.
- Morton, Thomas.** 1632. New English Canaan.
- Nichols, G. E.** 1913. The Vegetation of Connecticut: Virgin Forests. Torreyia **13**: 199-215, and Torreyia **14**: 188 (1914).  
1923. A Working Basis for the Ecological Classification of Plant Communities. Ecology **4**: 11-23; 154-179.
- Rhoads, S. N.** 1903. Mammals of Pennsylvania and New Jersey, p. 33. Describes effect on vegetation at "elk licks" where the activities of the elk resulted in *Crataegus* thickets.
- Smith, John.** 1616. A Description of New England.
- Society of American Foresters, New England Section, Committee on Research.** 1922. Forest Region and Type Classification for New England. Jour. of Forestry **20**: 122-129.  
1922. Revision of a Report of a Forest Region and Type Classification for New England. Jour. Forestry **20**: 795-798.
- Spaulding, V. M., B. E. Fernow, F. H. Chittenden, and F. Roth.** 1899. The White Pine. U. S. D. A., Forest Service Bul. 22.
- Temple, J. H.** 1889. History of Palmer, Massachusetts, p. 40.
- Thompson, Zadock.** 1824. A Gazetteer of the State of Vermont.  
1842. History of Vermont.
- Weaver, J. E., and F. E. Clements.** 1929. Plant Ecology.
- Williams, Samuel.** 1794. History of Vermont.
- Wood, William.** 1634. New England's Prospect.